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A Review of the *Pattonomys/Toromys* Clade (Rodentia: Echimyidae), with Descriptions of a New *Toromys* Species and a New Genus

LOUISE H. EMMONS[1] AND PIERRE-HENRI FABRE[2]

ABSTRACT

New phylogenomic analyses of South American arboreal echimyids show that there are three species within the genus *Toromys* (*T. grandis*, *T. rhipidurus*, and *T.* sp. nov.) and that the genera *Pattonomys* and *Toromys* form a clade that is the sister group to the other three genera of arboreal Echimyini (*Echimys, Makalata,* and *Phyllomys*). The arboreal echimyid species *Pattonomys occasius* is deeply divergent from other species of *Pattonomys* and from members of other extant named genera, although it shares a sister relationship with *Toromys*. We erect a new genus, *Leiuromys*, for it. To clarify the relationships among the species within these three genera, we describe them with molecular and morphological characters. Because most members of these genera have never been reviewed or diagnosed at the species level, we do so now, and we describe a new species, *Toromys albiventris,* from the upper Ucayali basin of Peru. We illustrate taxa and morphological features not before figured in publications.

INTRODUCTION

Echimyidae is one of the most morphologically and ecologically diverse mammalian families of Neotropical forests, but its classification has proved among the most difficult and problematic within Caviomorpha (Tate, 1935; Lara et al., 1996; Leite and Patton, 2002). Recent morphological (Emmons, 2005) and molecular inferences (Galewski et al., 2005; Fabre et al.,

[1] Division of Mammals, National Museum of Natural History, Smithsonian Institution; and Department of Mammalogy, American Museum of Natural History.
[2] Institut des Sciences de l'Évolution (ISEM, UMR 5554 CNRS), Université Montpellier II.

2013, 2014, 2016b; Upham et al., 2013; Upham and Patterson, 2015) have elucidated the long-standing enigma of the deep relationships among many genera of Echimyidae, and resolved some thorny phylogenetic questions with robust and well-supported hypotheses that both disentangled their phylogenetic histories and recovered unexpected relationships, such as the placement of the painted tree rat *Callistomys pictus* (Pictet, 1843) within Myocastorini (Loss et al., 2014; Fabre et al., 2016b). The clade Echimyini (sensu Fabre et al., 2016b) includes 13 of the 18 described genera of the Echimyinae in a radiation associated with an arboreal lifestyle, and it encompasses much of echimyid morphological diversity (Monteiro et al., 2005; Emmons et al., 2015a; Fabre et al., 2016a, 2016b), with striking ecomorphs such as the bamboo rats (*Dactylomys, Kannabateomys,* and *Olallamys* species) and the red-crested tree rat (*Santamartamys rufodorsalis*). All recent classifications have converged toward the following arrangement for these genera of arboreal lineages: (*Isothrix* (*Mesomys* + *Lonchothrix*)); ((*Diplomys* + *Santamartamys*) + (*Kannabateomys* (*Dactylomys* + *Olallamys*)); and ((*Toromys* + *Pattonomys*) + (*Makalata* + (*Echimys* + *Phyllomys*)) (Upham et al., 2013; Upham and Patterson, 2015; Fabre et al., 2016b). With molecular and morphological data, we examine below the species-level systematics of the *Toromys* + *Pattonomys* clade to better characterize these two divergent genera and their included species, all of which occur either in Amazonia or in the adjacent lowland forests of the Llanos and Caribbean littoral (fig. 1).

We use the phylogenomics-based higher level 1 classification of Fabre et al. (2016b: table 5), which splits the family Echimyidae into three subfamilies, Capromyinae, Euryzygomatomyinae, and Echimyinae. The Echimyinae includes two tribes, the largely terrestrial Myocastorini (*Callistomys, Hoplomys, Myocastor, Proechimys,* and *Thrichomys*), and the arboreal Echimyini (*Dactylomys, Diplomys, Echimys, Isothrix, Kannabateomys, Lonchothrix, Makalata, Mesomys, Olallamys, Pattonomys, Phyllomys, Santamartamys,* and *Toromys*). Although several nodes in the phylogeny remain unresolved, and thus those parts of the resulting classification are more weakly supported, the tribe Echimyini is always recovered as the same coherent clade of spiny or stiff-furred taxa (e.g., by Lara et al., 1996; Galewski et al., 2005; Upham et al., 2013; Loss et al., 2014; and Fabre et al., 2014, 2016b).

Species in the genera *Phyllomys, Pattonomys, Echimys,* and *Makalata* (including *grandis* and *rhipidura*) were segregated into monophyletic branches from other Echimyinae in a cladogram generated from morphological characters (Emmons, 2005: 270), but without resolution of basal intergeneric relationships. The genus *Pattonomys* was erected on the basis of this suite of morphological characters, especially of the teeth, but without genetic support or species-level diagnosis or analysis (Emmons, 2005). Subsequently, Emmons et al. (2015a) recognized four species from Colombia and northern Venezuela: *P. semivillosus, P. carrickeri, P. punctatus,* and the island form *P. flavidus,* as well as a morphologically and geographically divergent species from western Amazonia, *P. occasius,* which was provisionally consigned to *Pattonomys* because it shares more morphological characters with it than with any other genus (see also Patterson and Velazco, 2008), although it fails to agree in others.

Iack-Ximenes et al. (2005) erected the genus *Toromys,* to include only the giant rat, *T. grandis,* which had previously resided in *Makalata,* but the new genus was segregated without analysis of
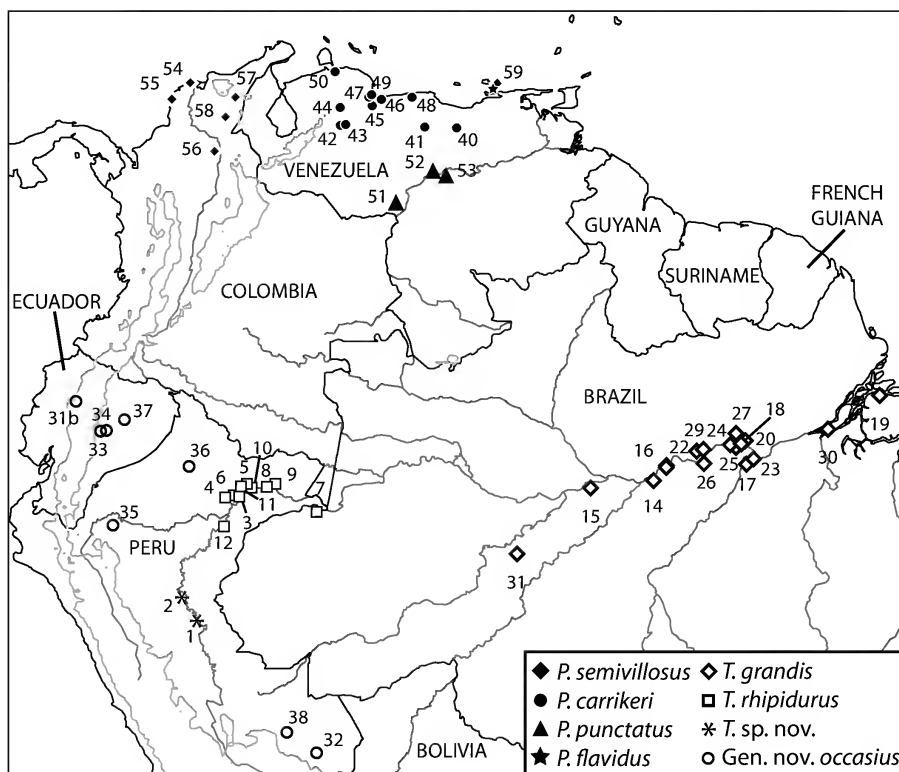
FIG. 1. Distribution of collecting localities for specimens examined in this report (some *Toromys grandis* localities are from Abreu-Júnior et al., 2017). Pale gray line represents the 2000 m elevation contour. Numbers are keyed to gazetteer entries (appendix 1)

genetic characters. Emmons (2005) concurrently referred *M. grandis*, *M. rhipidura*, and an undescribed species to an "*M. grandis* species group," based on morphological characters that distinguished them from other *Makalata*, but without further revision or phylogenetic hypothesis. Emmons et al. (2015b) subsequently placed *rhipidurus* in *Toromys*. We below provide morphological and molecular support for the expanded genus *Toromys*, and revise the diagnosis of the genus and its included species. Because multiple morphological characters of genera of Echimyini have been satisfactorily described and analyzed elsewhere (Carvalho and Salles, 2004; Leite, 2003; Emmons, 2005; Iack-Ximenez et al., 2005; Patterson and Velazco, 2006), we restrict our treatment to those features useful for the diagnosis of taxa within the *Pattonomys* + *Toromys* clade.

To provide a taxonomic and phylogenetic framework for the focal clade of this report, we used an integrative approach including both genetic and phenotypic data. With next-generation sequencing and molecular phylogenetic methods, we tested the monophyly of these genera and inferred the problematic relationships of *P. occasius*. Based on this new phylogenetic hypothesis we subsequently reexamined qualitative external and craniodental features. We now describe a new species of *Toromys* from the Ucayali region of Peru, identified long ago (Sanborn, 1949; Emmons, 2005), but previously lacking sufficient genomic and morphological support.

MATERIALS AND METHODS

Specimens examined: Specimens we examined and vouchers for tissues sequenced are housed in the following institutions: **AMNH,** American Museum of Natural History, New York; **BMNH,** Natural History Museum, London; **FMNH,** the Field Museum of Natural History, Chicago; **LSUMZ,** Louisiana State University Museum of Natural Science, Baton Rouge; **MBML,** Museu de Biologia Prof. Mello Leitão, Santa Teresa; **MCNM,** Museu de Ciências Naturais, Pontifícia Universidade Católica de Minas Gerais, Belo Horizonte; **MCNU,** Museu de Ciências Naturais, Universidade Luterana do Brasil, Canoas; **MCZ,** Museum of Comparative Zoology, Harvard University; **MN,** Museu Nacional, Universidade Federal (UF) do Rio de Janeiro, Rio de Janeiro; **MNHN,** Muséum National d'Histoire Naturelle, Paris; **MUSM,** Museo de Historia Natural, Lima; **MVZ,** Museum of Vertebrate Zoology, University of California, Berkeley; **MZUSP,** Museu de Zoologia, Universidade de São Paulo, São Paulo; **Naturalis,** Nationaal Natuurhistorisch Museum, Leiden; **NMW,** Naturhistorisches Museum, Vienna; **ROM,** Royal Ontario Museum, Toronto; **UFES-CTA**, Universidade Federal do Espirito Santo, Vitória, Brazil (-CTA tissue collection, -MAM mammal collection); **UFMG,** UF Minas Gerais, Belo Horizonte; **UFROM,** UF Rondônia, Porto Velho; **UM-ISEM,** University of Montpellier, Montpellier; and **USNM,** National Museum of Natural History, Smithsonian Institution, Washington, D.C. Localities for specimens are mapped (fig. 1) and listed in appendix 1, and DNA-sequenced specimens are indicated by asterisks (*) in "Specimens examined" at the end of taxon accounts.

Genomic taxon sampling: We sampled at least two specimens each for seven extant species of the genus *Toromys* and *Pattonomys*, including *T. grandis, T. rhipidurus, T. sp nov., P. carrikeri, P. punctatus, P. semivillosus,* and *P. occasius.* We obtained DNA from both museum specimens and fresh tissues stored in the museums listed above. We sequenced complete mitogenomes for nine taxa representing most species of *Toromys* and *Pattonomys*, but we obtained only a few base pairs (50–100 bp) for *P. flavidus,* and so do not include it in the analysis. We gathered some data from the National Center for Biotechnology Information (NCBI) published by Fabre et al. (2016b), and when possible selected sequences obtained from voucher specimens for which mitogenomic sequences were available (table 1). Exemplar species of the following genera were used as outgroups for phylogenetic analysis: *Echimys, Makalata, Phyllomys, Kannabateomys, Olallamys, Dactylomys, Isothrix, Mesomys, Lonchothrix, Diplomys,* and *Santamartamys.* We also included three newly sequenced species of Echimyini: *Echimys saturnus, Makalata macrura, Isothrix pagurus,* and several other Echimyidae as more distant outgroups, to stabilize the arboreal echimyid relationships. We also downloaded published cytochrome-*b* (*cyt-b*) data for *Toromys* and *Pattonomys* (Upham and Patterson, 2015) to estimate molecular distance among species and potential populations.

Sequencing and assembly of complete mitochondrial genomes: Twelve samples of dried tissue harvested from specimens were stored in Eppendorf tubes, which were processed in the "Degraded DNA Facility" in Montpellier, France (dedicated to processing low-quality/quantity DNA tissue samples). An alcohol-preserved sample of fresh tissue was available for one other taxon (*Pattonomys carrikeri* ROM 107955), already published by Fabre et al. (2016b). The DNA from museum skin samples was extracted in a separate room of the laboratory to avoid contamination. DNA was extracted using the DNeasy Blood and Tissue Kit (Qiagen)

TABLE 1. Species, museum voucher specimen number, tissue collection number (if different) or collector's field number, published reference, GenBank *cyt-b* mitogenome accession number, and source tissue used for molecular comparisons. Boldface entries were newly sampled for this report. Some additional information may be retrieved online (vertnet.org).

Taxon	Voucher number	Tissue number	Publication	Accession mitogenome	Tissue sampled
Ctenomys rionegrensis	—	—	Tomasco and Lessa (2011)	HM544130.1	fresh tissue
Octodon degus	—	—	Tomasco and Lessa (2011)	HM544134.1	fresh tissue
Spalacopus cyanus	—	—	Tomasco and Lessa (2011)	HM544133.1	fresh tissue
Tympanoctomys barrerae	—	—	Tomasco and Lessa (2011)	HM544132.1	fresh tissue
Proechimys longicaudatus	—	—	Tomasco and Lessa (2011)	HM544128.1	fresh tissue
Trinomys dimidiatus	—	—	Voloch et al. (2013)	JX312694.1	fresh tissue
Callistomys pictus	UFMG	RM-233	Fabre et al. (2016b)	KU892754	fresh tissue
Capromys pilorides	MVZ 191417	—	Fabre et al. (2016b)	KU892766	fresh tissue
Carterodon sulcidens	MZUSP 34766	APC 1082	Fabre et al. (2016b)	KU892752	fresh tissue
Clyomys laticeps	MCNM 2009	—	Fabre et al. (2016b)	KU892753	fresh tissue
Dactylomys dactylinus	UFROM 339	—	Fabre et al. (2016b)	KU762015	fresh tissue
Diplomys labilis	USNM 335742	—	Fabre et al. (2016b)	KU892776	dry skin
Echimys chrysurus	UM-ISEM	T-3835	Fabre et al. (2016b)	KU892781	fresh tissue
Euryzygomatomys spinosus	UFMG 1948	CTA-102	Fabre et al. (2016b)	KU892755	fresh tissue
Geocapromys browni	Naturalis MAM 23884	—	Fabre et al. (2016b)	KU892767	dry skin
Geocapromys ingrahami	USNM 395696	—	Fabre et al. (2016b)	KU892768	dry skin
Hoplomys gymnurus	MVZ 225082	—	Fabre et al. (2016b)	KU892779	fresh tissue
Isothrix sinnamariensis	UM-ISEM	T-4377	Fabre et al. (2016b)	KU892785	fresh tissue
Kannabateomys amblyonyx	MBML 3001	—	Fabre et al. (2016b)	KU892775	fresh tissue
Lonchothrix emiliae	FMNH 140821	—	Fabre et al. (2016b)	KU892786	dry skin
Makalata didelphoides	UM-ISEM	T-5023	Fabre et al. (2016b)	KU892782	fresh tissue
Mesocapromys melanurus	MCZ 34406	—	Fabre et al. (2016b)	KU892769	dry skin
Mesomys hispidus	UM-ISEM	T-6523	Fabre et al. (2016b)	KU892787	fresh tissue
Mesomys stimulax	Naturalis MAM 21728	—	Fabre et al. (2016b)	KU892788	dry skin
Myocastor coypu	UM-ISEM	T-0245	Fabre et al. (2016b)	KU892780	fresh tissue
Mysateles prehensilis gundlachi	MCZ 17090	—	Fabre et al. (2016b)	KU892770	dry skin
Olallamys albicauda	USNM 241343	—	Fabre et al. (2016b)	KU892774	dry skin
Phyllomys blainvillii	MVZ 197568	CTA-1205	Fabre et al. (2016b)	KU892756	fresh tissue
Phyllomys dasythrix	MCNU 844	AC-628	Fabre et al. (2016b)	KU892757	fresh tissue

Taxon	Voucher number	Tissue number	Publication	Accession mitogenome	Tissue sampled
Phyllomys lundi	MN 62392	CTA-881	Fabre et al. (2016b)	KU892758	fresh tissue
Phyllomys mantiqueirensis	MN 62393	CTA-912	Fabre et al. (2016b)	KU892759	fresh tissue
Phyllomys pattoni	MN 62391	CTA-984	Fabre et al. (2016b)	KU892760	fresh tissue
Plagiodontia aedium	Naturalis MAM 3865	—	Fabre et al. (2016b)	KU892771	dry skin
Proechimys cuvieri	UM-ISEM	T-5765	Fabre et al. (2016b)	KU892778	fresh tissue
Proechimys roberti	UFMG 3031	CTA-1524	Fabre et al. (2016b)	KU892772	fresh tissue
Santamartamys rufodorsalis	AMNH 34392	—	Fabre et al. (2016b)	KU892777	dry skin
Thrichomys apereoides	MVZ 197573	—	Fabre et al. (2016b)	KU892773	fresh tissue
Toromys grandis	FMNH 92198	—	Fabre et al. (2016b)	KU892784	dry skin
Trinomys albispinus	MN 30526	AL-3054	Fabre et al. (2016b)	KU892761	fresh tissue
Trinomys iheringi	UFES MAM 2230	ROD-156	Fabre et al. (2016b)	KU892762	fresh tissue
Trinomys paratus	UFES MAM 639	CTA-588	Fabre et al. (2016b)	KU892763	fresh tissue
Trinomys setosus	UFES MAM 2043	CTA 3578	Fabre et al. (2016b)	KU892764	fresh tissue
Trinomys yonenagae	MZUSP	PEU-880027	Fabre et al. (2016b)	KU892765	fresh tissue
Pattonomys occasius	**MCZ 37964**	—	**this paper**	**MG963136[a]**	**dry skin**
Pattonomys occasius	FMNH 84529	—	Upham & Patterson (2015)	KJ742661[b]	dry skin
Toromys rhipidurus	**AMNH 73277**	—	**this paper**	MG963137[a]	**dry skin**
Toromys rhipidurus	**AMNH 74086**	—	**this paper**	**MG954078**	**dry skin**
Toromys rhipidurus	FMNH 87244	—	Upham & Patterson (2015)	KJ742663[b]	dry skin
Toromys sp. nov.	**AMNH 98666**	—	**this paper**	MG963134[a]	**dry skin**
Toromys sp. nov.	**LSUMZ T8222**	—	**this paper**	**MG954077**	**dry skin**
Pattonomys punctatus	**AMNH 29872**	—	**this paper**	**MG954074**	**dry skin**
Pattonomys punctatus	**USNM 374742**	—	**this paper**	**MG954075**	**dry skin**
Pattonomys carrikeri	**USNM 456444**	—	**this paper**	**MG963787**	**dry skin**
Pattonomys carrikeri	ROM 107955	—	Fabre et al. (2016b)	KU892783	fresh tissue
Pattonomys semivillosus	**USNM 280204**	—	**this paper**	**MG954076**	**dry skin**
Echimys saturnus	**MCZ 41569**	—	**this paper**	**MG954072**	**dry skin**
Makalata macrura	**LSUMZ T8221**	—	**this paper**	**MG954073**	**dry skin**
Isothrix pagurus	**MCZ 30865**	—	**this paper**	**MG963135[a]**	**dry skin**

[a] Due to 3% missing data, additional sequences of individual genes for these four samples are found under MG963114–MG693160.

[b] *Cyt-b* comparison only.

following the manufacturer's instructions, with two final elutions in water. These museum skin samples were extracted separately, along with a negative control for each batch to monitor possible contamination. The DNA was fragmented by sonication using an ultrasonic cleaning unit (Elmasonic). The 3′ ends of the obtained fragments were then repaired and filled before being ligated with adaptors and tagged according to a custom, cost-effective version of the Meyer and Kircher (2010) protocol for Illumina library preparation (Tilak et al., 2015). Tagged DNA libraries were pooled and sequenced by the GATC–Biotech company (Konstanz, Germany) on Illumina HiSeq 2000 lanes.

Raw 101-nt reads were imported in Geneious R10 (Kearse et al., 2012), and adaptor fragments were removed by the "trim ends" utility. Then a mapping of the reads on the phylogenetically closest available mitochondrial genome was performed for each species. The following mapping parameters were used in the Geneious read mapper: a minimum of 24 consecutive nucleotides (nt) perfectly matching the reference, a maximum 5% of single nt mismatch over the read length, a minimum of 95% nt similarity in overlap region, and a maximum of 3% of gaps with a maximum gap size of 3 nt. Iterative mapping cycles were performed to elongate the sequence when the complete mitogenome was not recovered after the initial mapping round. A high-quality consensus was generated and the circularity of the mitogenome was verified by the exact superimposition of the 100 nucleotides at the assembly extremities. The number of satellite repetitions in the control region (CR) is an estimate, as there were Illumina reads that entirely contained repeats, making it difficult to determine the exact copy number.

DNA SUPERMATRICES AND PHYLOGENETIC ANALYSIS: We combined our newly obtained mitogenomes with sequences previously made available from our mitogenomic database (Fabre et al., 2016b). Complete mitogenomes were subsequently aligned with MUSCLE (Edgar, 2004), as implemented in Seaview v4.5.2 (Gouy et al., 2010), and with Macse v1.3 (Ranwez et al., 2011). Ambiguous regions of the alignments were cleaned with trimAl v1.2 (Capella-Gutiérrez et al., 2009). We obtained one nucleotide dataset comprising 32 complete mitogenomes (15,626 sites, 3% of missing data; table 1). Maximum likelihood and Bayesian inferences were subsequently computed on this dataset following the protocol of Fabre et al. (2016b) using RaXML software (Stamatakis, 2006) and PhyloBayes 3 (Lartillot et al., 2009), which allow implementation of the CAT mixture model (Lartillot and Philippe, 2004). Relative exchangeabilities among nucleotides were described under the GTR model. To account for among-site heterogeneity in the nucleotide substitution rates, we used a Gamma distribution with 4 discrete categories (G_4) in both analyses. For the Bayesian analysis, two Markov-chain Monte Carlo analyses were run with PhyloBayes 3 for 10,000 cycles (ca. 8,000,000 generations) with trees sampled every 5 cycles after discarding the first 1000 as a burnin. Convergence was ensured when the maximum difference in bipartition frequencies as estimated by the two chains was below 0.1. Node supports were estimated by 1000 bootstraps for the ML analysis, and by posterior probabilities (PP) measured for the Bayesian post-burnin analysis.
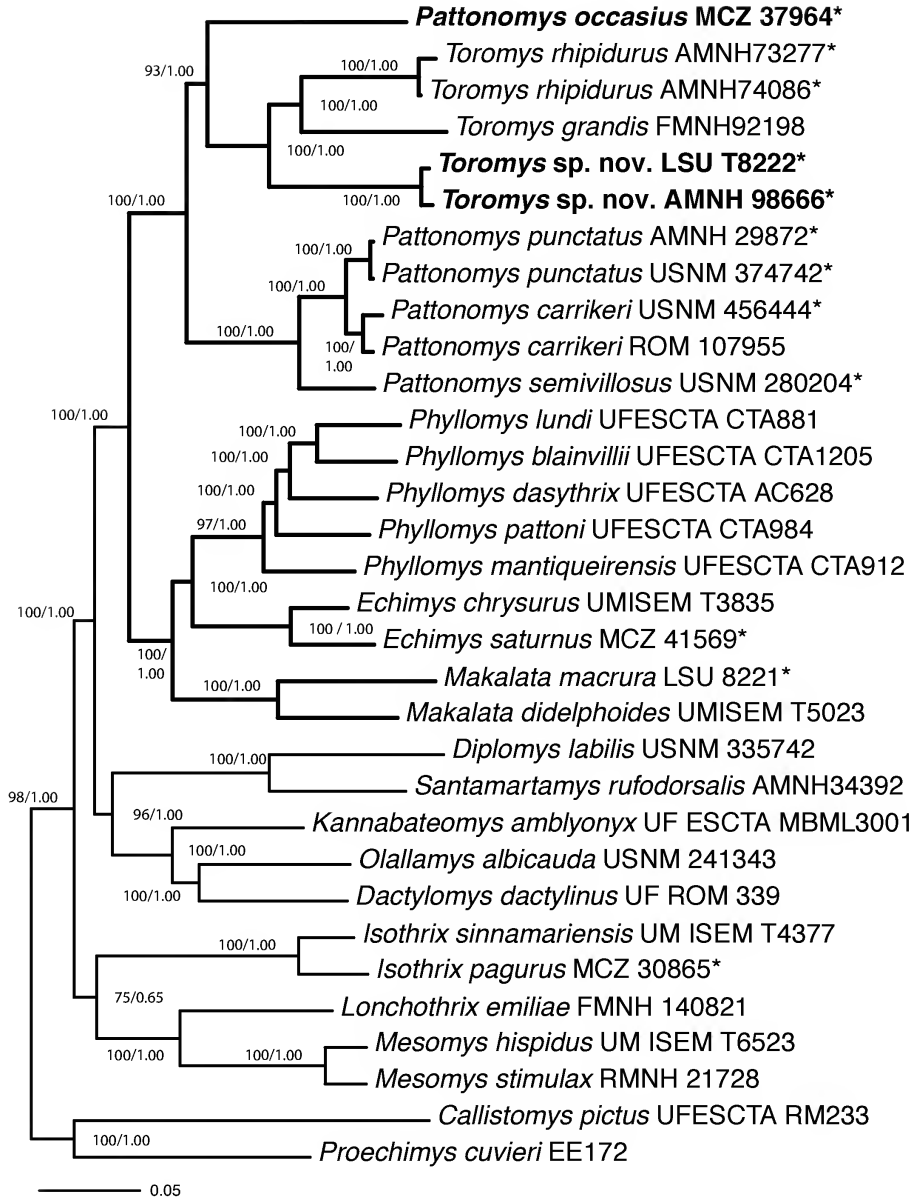
FIG. 2. PhyloBayes maximum credibility tree based on mitogenomic data. Nodal support is indicated with bootstrap (RaXML analysis) on the left and posterior probabilities (PhyloBayes analysis) on the right; the values are separated by /.

MORPHOMETRIC PROCEDURES: Standard cranial measurements were made with digital calipers. Measurements taken and age classes were as defined and illustrated in Patton and Rogers (1983) and Emmons (2005), with the addition of a measurement of width of the palate between the posterior roots of M1. We follow Woods and Howland (1979) for cranial nomenclature. As echimyid rodents have indeterminate growth (Patton and Rogers, 1983), we measured only adults of age classes 8 to 10.

TABLE 2. Uncorrected *cyt-b* distances (scaled as percent sequence divergence; below diagonal) and K2P-corrected distances (above diagonal) among taxa in the *Toromys/Pattonomys* clade. Diagonal elements (bolded) are average uncorrected pairwise distances between conspecific sequences.

		1	2	3	4	5	6	7
1.	*Pattonomys occasius*	**2.0**	19.1	15.2	21.1	14.1	13	10.7
2.	*Toromys grandis*	12.8	–	16.8	17.5	23.0	21.3	19.2
3.	*Toromys rhipidurus*	8.6	8.5	**0.3**	12.8	18.8	16.0	14.4
4.	*Toromys* sp. nov	11.1	12.8	7.9	**1.4**	21.1	22.3	20.7
5.	*Pattonomys semivillosus*	11.6	12.1	9.4	13.1	**0.4**	6.9	6.1
6.	*Pattonomys punctatus*	12.5	14.0	10.1	16.6	6.7	**0.7**	4.5
7.	*Pattonomys carrikeri*	12.6	14.0	14.3	16.3	7.0	4.3	**1.1**

ANALYTIC RESULTS

MITOGENOMIC RESULTS: Our mitogenomic analysis (fig. 2) corroborates the generic relationships previously reported by Fabre et al. (2016a, 2016b) and resolves additional relationships at the species level. Among other results, the Amazonian spiny- or stiff-furred arboreal Echimyini form two clades: ((*Echimys* + (*Phyllomys* + *Makalata*)) on the one hand and (*Pattonomys* + *Toromys*) on the other. As can be seen, *Pattonomys occasius* is the sister taxon to *Toromys* and is not closely allied to other *Pattonomys* species, from which it differs by about 10%–14% in pairwise comparisons of *cyt-b* sequences (table 2). There is thus no molecular support for its classification within the latter genus, for which it also lacks convincing morphological support. Cytochrome-*b* divergence of *P. occasius* from *Toromys* is likewise high (about 9%–13%, uncorrected; table 2) and comparable to the range of divergence values found among other echimyine genera (usually >10%). Given these genetic results, its Amazonian distribution, and morphologically diagnostic comparisons to be described below, we provide a new generic name for "*P.*" *occasius* in the following taxonomic accounts.

Additional relationships resolved by our analysis include the monophyly of *Toromys* and the sister-group relationship of *T. rhipidurus* + *T. grandis* with the distinctive *T.* sp. nov., all of which differ substantially from one another in pairwise sequence comparisons (table 2). *Pattonomys semivillosus*, *P. carrikeri*, and *P. punctatus* are likewise confirmed as a clade, with the geographically disjunct *P. semivillosus* as the most genetically divergent (table 2) and sister to the two other sampled species.

As well as by genetic distinctiveness, both new taxa described below are diagnosable and distinguished from their nearest known relatives by morphological traits. Moreover, the genus *Toromys* would not be diagnosable by any of its most striking characters of pelage and dentition if "*Pattonomys*" *occasius* were to be included within it. Likewise, *Pattonomys* has a unique and diagnostic cheektooth occlusal pattern that differs strikingly from that of both "*P.*" *occasius* and all *Toromys* species.

Finally, our analysis includes, for the first time, *Echimys saturnus*, a rare endemic lineage from the Andean piedmont. This lineage is recovered as the sister taxon of *Echimys chrysurus* (1.6% of *cyt-b* divergence), validating the generic diagnoses proposed by Emmons (2005) and Emmons et al. (2015a).

FIG. 3. *Leiuromys occasius* BMNH 21.2.15.6, holotype skin, dorsal and ventral. The colors of this skin are much more saturated rusty/dark than are those of most others examined, which could be faded.

TABLE 3. Selected external characters of species in the *Pattonomys/Toromys* clade.

	Pattonomys				Toromys			Leiuromys
	semivillosus	carrikeri	punctatus	flavidus[a]	grandis	rhipidurus	sp. nov.	occasius
Aristiform spines	wide, stiff, pointed	wide, stiff, pointed	wide, stiff, pointed	wide, stiff, pointed	narrow, with blunt or hairlike tips	narrow, with hairlike tips	mostly narrow, with hairlike tips	wide, stiff, pointed
Ventral coloration[b]	white or buff	grayish, white, or buff	white	white	gray-brown	gray-brown	white or pale gray	bright buff
Underfur	fine bristles, ochraceous	fine bristles, ochraceous	fine bristles, ochraceous	fine bristles, ochraceous	rare fine bristles	rare fine bristles	rare fine bristles	fine, wavy, rusty
Tail hairs[c]	moderate, salient	moderate, salient	moderate, salient	—	dense, long	dense, long	dense at base	short, adpressed
Tail scales[d]	square	nearly hexagonal	squareish	—	—[e]	long, squareish[f]	long, hexagonal[f]	short, hexagonal
Postauricular markings[g]	large, white tufts	large, pale-gray tufts	inconspicuous gray tufts	gray tufts?	white skin	absent	absent	absent
Digital pad 1	round?	elongate	elongate	—	round	round	round?	round
Digital pad 3	large, elongate	small, elongate	small, triangular?	large, triangular?	small, round	small, round	triangular?	small, round

[a] The single specimen we examined is missing its tail, so characters of that organ could not be scored.
[b] Predominant coloration of the underparts, not including contrasting blazes or blotches of other color.
[c] "Salient" caudal hairs are curved outward; "adpressed" hairs lie flat against the skin.
[d] Tabulated entries describe scale shape on the dorsal surface near the base of the tail. Square (or squareish) scales are arranged in transverse rows (rings) around the tail, whereas hexagonal (or nearly hexagonal) scales form diagonal (spiral) series.
[e] Scales obscured by dense hairs.
[f] With curved (convex) posterior margins.
[g] Tufts of fur or skin behind the ear that contrast in color with surrounding fur.

TABLE 4. Selected cranial and dental characters of species in the *Pattonomys/Toromys* clade.

	Pattonomys				Toromys			Leiuromys
	semivillosus	*carrikeri*	*punctatus*	*flavidus*	*grandis*	*rhipidurus*	sp. nov.	*occasius*
Buccinator and masticatory foramina	separate	joined	separate	separate	separate	separate	separate	joined
Incisor color[a]	pale yellow	pale yellow	orange	white	orange	orange	pale yellow	white
Lophs on p4	four	four	four	four	five	five	five	four
Lophs on M3	four	four	four	four	four	four	four	three
Unworn M1-2 mure[b]	center	center	center	center	absent	absent	absent	lingual edge
M1 posteroflexus[c]	short	short	short	short	long	long	short	short
M2 protoloph	short[d]	short[d]	short[d]	short[d]	crosses tooth	nearly crosses tooth	nearly crosses tooth	nearly crosses tooth
M1-M2 lingual fosettes[e]	two	two	two	two	two	two	two	one
Posterior border of lower molars	straight	straight	straight	straight	straight	straight	straight	curved

[a] Pigmentation of upper incisor enamel.
[b] Position on occlusal surface (if present).
[c] A "long" posteroflexus crosses 80% of tooth, a "short" posteroflexus crosses only 60% of tooth.
[d] "Short" M2 protolophs extend only about halfway across the tooth.
[e] On heavily worn teeth.

TABLE 5. External measurements (mm) of *Leiuromys, Pattonomys,* and *Toromys.*[a]

Species	Head and body	Tail	Hind foot	Ear	Weight
Leiuromys occasius	211 (205–218, 2)	223 (220–225, 2)	36 (36–37,2)	14 (14–15, 2)	—
Pattonomys carrikeri	202 (135–264, 37)	225 (181–261, 32)	38 (35–44, 37)	16 (11–22, 36)	285 (194–416, 7)
P. flavidus	252 (1)	248 (1)	40 (1)	—	—
P. punctatus	241 (218–268, 3)	230 (222–234, 3)	40 (34–43,3)	20 (19–22, 3)	421 (407–435, 2)
P. semivillosus	217 (207–227, 2)	220 (218–222, 2)	39 (38–39, 2)	19 (18–19, 2)	—
Toromys sp. nov.	221 (210–230, 7)	193 (180–205, 7)	35 (31–37, 7)	14 (11–17, 7)	315 (1)
T. grandis	307 (253–353, 68)	284 (200–340, 68)	57 (50–63, 67)	—	—
T. rhipidurus	237 (212–260, 8)	199 (180–215, 7)	42 (37–49, 8)	15 (12–17, 8)	—

[a] Tabulated statistics are the sample mean and (in parentheses) the observed range and sample size. Note that Five of seven *Leiuromys occasius* specimens we examined lacked external measurements. Measurements of another series of *Toromys grandis* are found in Iack-Ximenez et al. (2005).

TAXONOMIC ACCOUNTS

The following accounts formalize taxonomic changes consistent with our analytic results (above), describe new taxa, and summarize qualitative character information and measurement data to facilitate specimen identifications. Because full synonymies of all currently recognized echimyid species and genera were previously provided by Emmons et al. (2015a), we do not reiterate them here.

Leiuromys, new genus

TYPE SPECIES: *Echimys occasius* Thomas, 1921: 450.

CONTENTS: Only the type species.

ETYMOLOGY: From the Greek *leios* ("smooth, bald") and *uros* ("tail"), thus, "bald-tailed mouse," in reference to the slick, hairless appearance of the tail, which is more naked than that of any other arboreal echimyine except lowland species of *Dactylomys*.

DIAGNOSIS: Small, arboreally adapted brown rats, heavily spined dorsally with abundant wide, sharp, spines on midback from neck to rump, spines intermixed with fine wavy rust-red underhairs (fig. 3; tables 3–6). Tail hairs short, fine, and inconspicuous, so that the tail looks bare and even shiny. Auditory tympanic bullae small, flattened in lateral aspect. Inferior jugal process reduced to nearly absent, but jugal fossa deep and sharply pointed anteriorly. Masticatory and buccinator foramina joined in a single aperture. Incisors bone white; upper incisor root does not extend to within the maxillary base of the zygoma. Lower premolars tetralophodont. Third upper molars trilophodont. The hypoflexids on m1–m3 fall nearly opposite the middle of the mesolophids, such that the teeth viewed from the lingual side are nearly symmetrical, rounded M-shapes. Upper lingual and lower labial hypoflexi short and wide, about a quarter of the width of tooth, but labial meso- and metaflexi long, such that when worn to a mure in M1 and M2, the mure is on the far lingual edge of the tooth. All mandibular cheek-teeth have curved posterior borders.

TABLE 6. Cranial measurements (mm) of *Leiuromys*, *Pattonomys*, and *Toromys*. Tabulated statistics include the sample mean and (in parentheses) the observed range and the sample size.

|	*L. occasius*	*P. carrikeri*	*P. flavidus*	*P. punctatus*	*P. semivillosus*	*T. grandis*	*T. rhipidurus*	*T.* sp. nov.
Skull greatest length	49.39 (47.9–50.8, 5)	53.2 (50.6–58.3, 23)	-	56.9 (55.4–58.9, 8)	50.9 (50.6–51.3, 2)	68.3 (64.6–73.1, 35)	56.53 (52–59.1, 15)	52.4 (51.6–54.2, 7)
Zygomatic breadth	23.3 (22.0–25.2, 5)	24.3 (20.9–26.2, 22)	26.1	27.1 (25.7–28.7, 8)	23.9 (23.8–24.1, 2)	31.2 (25.4–32.7, 34)	27.4 (25.7–29.2 15)	23.7 (22.8–24.5, 7)
Palatal length A	18.3 (16.9–19.3, 5)	21.3 (19.3–23.4, 22)	22.1	24.1 (23.2–24.8, 8)	19.8 (19.5–20.2, 2)	29.2 (26.6–30.9, 35)	22.6 (20.5–24.9, 16)	20.6 (19.0–21.3, 7)
Palatal length B	8.4 (6.9–9.2, 5)	10.2 (8.8–11.4, 22)	10.6	11.8 (10.7–12.8, 8)	9.9 (9.5–10.3, 2)	13.5 (12.4–14.7, 35)	11.5 (10.2–12.4, 16)	10.0 (9.2–10.7, 7)
Mastoid breadth	19.2 (18.2–20.1, 5)	20.6 (19.3–22.1, 22)	20.4	21.9 (21.0–23.0, 8)	20.3 (20.2–20.4, 2)	25.7 (20.2–27.4, 35)	22.14 (20.8–23.5, 14)	20.2 (19.2–21.7, 7)
Rostral breadth	7.2 (6.2–7.9, 5)	7.9 (7.2–8.5, 22)	8.7	9.2 (8.7–10.1, 8)	7.7 (7.7–7.7, 1)	11.0 (9.9–11.6, 34)	8.7 (7.8–9.2, 16)	7.7 (7.2–8.0, 7)
Basilar length of Hensel	37.3 (35.6–39.0, 4)	40.5 (37.8–43.8, 22)	—	44.3 (43.0–45.4, 8)	42.4 (39.0–45.8, 2)	53.9 (50.3–56.8, 33)	43.15 (38.–47, 13)	39.6 (38.7–40.1, 5)
Cranial depth	15.2 (14.7–15.6, 4)	16.2 (15.0–18.4, 22)	17	17.0 (15.3–19.5, 7)	17.0 (17.0–17.0, 1)	18.4 (17.2–19.7, 32)	16.69 (15.6–17.5, 14)	15.6 (14.8–16.0, 7)
Rostral depth	10.0 (8.4–10.7, 5)	11.1 (10.1–11.8, 22)	12	12.4 (11.9–13.0, 8)	11.0 (11.0–11.1, 2)	15.3 (13.5–16.6, 35)	12.7 (11.4–13.9, 16)	11.2 (10.3–11.7, 7)
Maxillary toothrow	9.7 (7.3–10.8, 5)	11.4 (10.7–12.5, 22)	12.7	12.5 (11.8–13.4, 5)	11.6 (11.4–11.8, 2)	15.7 (14.4–16.9, 35)	13.2 (12.2–14.2, 16)	11.1 (10.1–11.9, 7)
Nasal length	15.1 (13.2–16.9, 5)	17.1 (14.7–19.5, 22)	16.9	17.2 (16.2–19.1, 8)	16.5 (16.4–16.7, 2)	22.5 (19.6–24.8, 35)	17.61 (14.7–19.3, 15)	17.1 (16.2–18.9, 6)
Least interorbital constriction	11.4 (10.3–12.9, 5)	13.1 (11.9–13.7, 21)	15.3	14.7 (12.5–16.4, 8)	13.3 (12.7–13.9, 2)	18.4 (16.5–20.4, 34)	15.2 (13.6–17, 16)	13.5 (12.4–14.6, 6)
Rostral length	16.4 (14.7–17.6, 5)	19.6 (17.7–21.9, 22)	19.8	20.4 (19.7–21.6, , 8)	18.1 (17.6–18.6, 2)	26.1 (21.0–28.6, 35)	20.05 (17–21.5, 15)	18.0 (16.9–19.7, 6)
Maxillary breadth	6.5 (6.1–7.2, 4, 5)	7.0 (5.6–8.0, 22)	7.3	7.6 (7.0–8.1, 7)	7.2 (7.2–7.2, 1)	10.2 (8.8–19.4, 35)	8.567 (7.5–9.3, 15)	7.0 (6.2–7.5, 6)
Diastema length	10.4 (9.6–11.4, 5)	11.7 (10.8–12.8, 22)	12	12.9 (12.4–13.9, 8)	10.9 (10.4–11.3, 2)	16.3 (14.5–17.6, 35)	11.8 (10.5–12.9, 16)	11.0 (10.6–11.6, 7)
Bullar Length	9.7 (8.7–10.5, 5)	12.1 (11.2–13.0, 22)	10.6	12.7 (11.9–13.5, 8)	12.0 (12.0–12.0, 2)	12.7 (11.2–13.9, 35)	10.5 (9–12.2 16, 16)	10.1 (9.4–10.7, 7)
Postpalatal Length	23.2 (21.9 23.7, 5)	23.4 (18.2–27.8, 21)	—	24.4 (23.0–26.5, 8)	22.6 (22.2–22.9, 2)	27.8 (23.6–30.7, 35)	24.71 (24–25.8, 13)	23.6 (23.3–23.6, 5)
Molar width	1.4 (0.9–1.8, 5)	2.1 (1.6–2.7, 22)	1.9	2.2 (1.6–3.0, 8)	2.1 (1.9–2.2, 2)	2.7 (2.0–3.8, 35)	—	1.8 (1.6–2.2, 4)
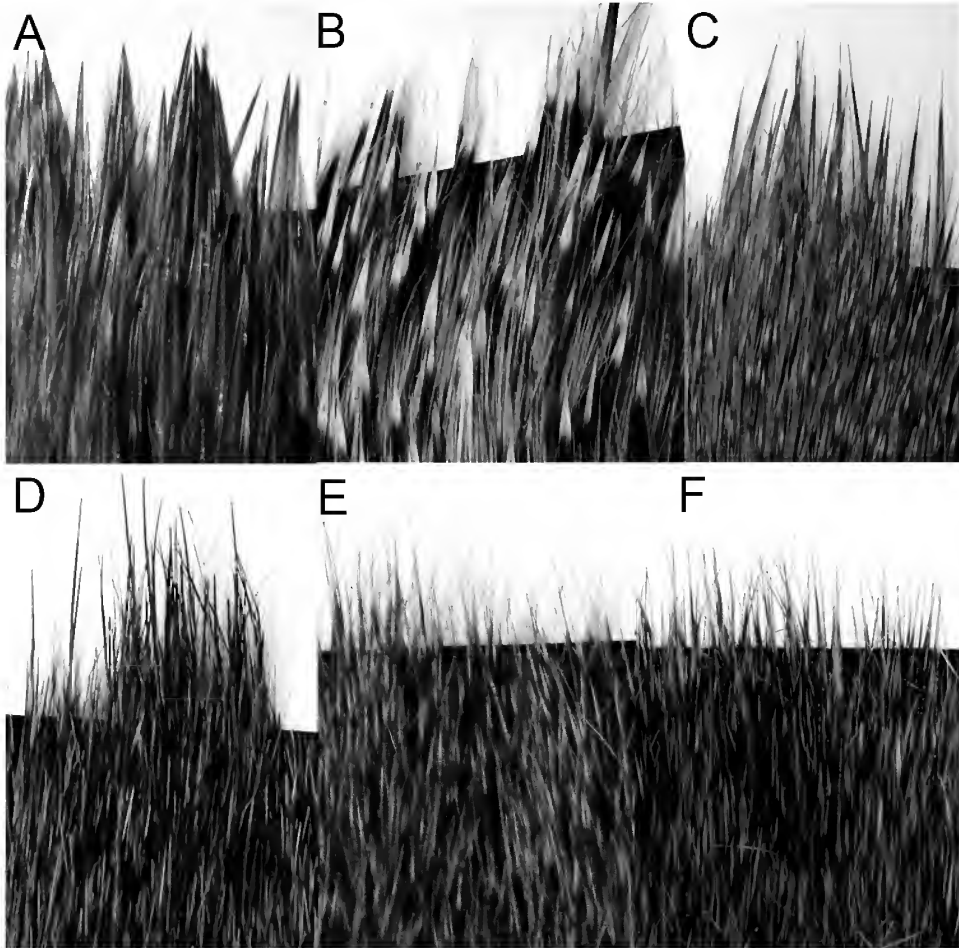
FIG. 4. Pelage of dorsum at rump. **A,** *Leiuromys occasius.* FMNH 84529, high density of sharply pointed spines and fine, wavy red underhairs; **B,** *Pattonomys semivillosus* USNM 280204, dense, more tapered, white-tipped spines, abundant pale bristles, straight ochraceous underhairs; **C,** *Makalata* cf. *didelphoides* USNM 549593, agouti pelage, sparser narrowly buff-tipped spines, tapered hairlike spine tips; **D,** *Toromys grandis* AMNH 94036, thick bristles, no spines; **E,** *T. rhipidurus* AMNH 73273, fine-banded agouti bristles; **F,** *T.* sp. nov., narrow aristiforms and a few narrow spines with hairlike tips, abundant thin, agouti bristles. The resemblance between *Toromys* congeners is evident. Spine tips are more sharply tapered in A than in B.

DESCRIPTION: Upperparts with abundant, wide, strong spines on midback from neck to rump, spines intermixed with fine, wavy, rust-red underhairs that show through aristiforms, giving back a rusty hue (fig. 3). Spine tips sharp, narrowing abruptly, with short microscopic hairlike processes at tips (fig. 4A). Spines tipped with pale buff sparsely speckle the sides of the hindquarters and tail base. Dorsal spines pale gray-brown at base, with a dusky band, a narrow, subterminal pale whitish or buffy band, and dusky, buff, or black-brown tips (fig. 4A). Upperparts uniform light ochraceous brown, between Cinnamon and Sayal Brown (Smithe, 1975), lined with dusky, or blackish Dusky Brown (the holotype and AMNH 71897). The spines on the middorsum from neck to rump are the darkest and nearly unbanded (figs. 3, 4A). Head
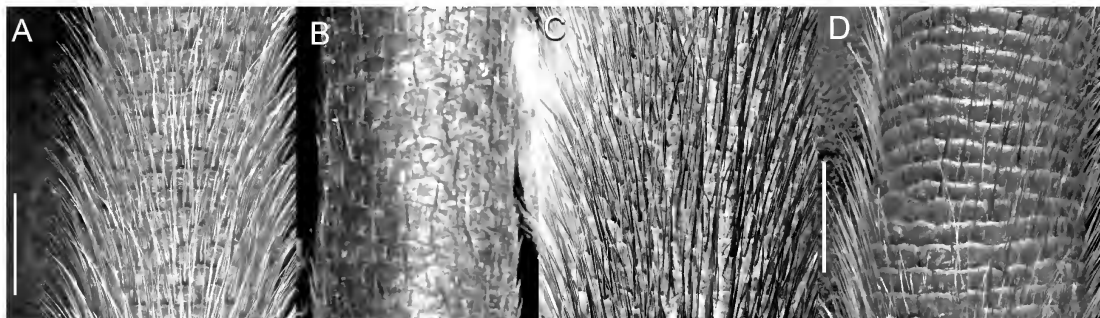
FIG. 5. Scales and hairs on dorsal tail base. **A,** *Pattonomys carrikeri* USNM 496483, irregular scales nearly square or slightly hexagonal, hairs unicolored, long, and curled outward; **B,** *Leiuromys occasius* FMNH 84259, short, wide hexagonal scales in spiral rows, short, adpressed, scalelike hairs in pairs; **C,** *Toromys rhipidurus* AMNH 276710, scales rounded posteriorly, about as long as wide, hairs robust, unicolor, black or rusty; **D,** *Makalata macrura* USNM 496480, short, rectangular scales in even rows, fine, salient hairs that are often banded dark at base, pale at tips. White scale bars 5 mm, fluid-fixed specimens except B.

and muzzle brown above, without any red color. Cheeks below the ears, forelimbs, and hindlimbs tinged grayish. Feet pale beige to rusty above; silvery ungual tufts reach to the ends of the claws. Ventral pelage of soft aristiforms, colored strong to pale buff, grading gradually from the sides (fig. 3); inner thighs slightly darker pinkish buff; the chest and lower abdomen and inguinal regions can have self-white patches, including the tail base, or are crossed by a white band between the elbows. Vibrissae black, moderately robust and the longest reaches to the shoulder. Ears short, pigmented, and nearly naked, lined with a few wispy, dusky hairs. Tail slightly longer than head and body length, brown pigmented, with a naked and somewhat shiny appearance. Dorsal hair ends abruptly close to the body at the tail base; distal tail hairs inconspicuous and closely adpressed. Scales on the tail base evenly hexagonal, wider than long, tapered at the lateral ends. Dorsally each scale has one robust, scalelike dark hair about two and a half scale rows long, and one shorter, fine, hair (fig. 5B). Ventrally, tail hairs somewhat longer (three scale rows), adpressed, and silvery. An adult female (FMNH 84259) has two used lateral pairs of mammae spaced about evenly between the limbs and 1.5 cm into the dorsal pelage field, and possibly an unused inguinal pair. As far as can be seen on dried specimens, the feet have small digital pads collared with rings of tubercles as in *Toromys* species (fig. 6A), and with numerous plantar tubercles on the bottom and sides of the feet around the pads. Cranium lightly built for the subfamily, inferior jugal process much reduced or essentially absent (figs. 7D, 8, 9D, 10D). Mastoid processes are short, reach to the middle of the auditory meatus, and are adpressed to the cranium; the space above the auditory meatus is nearly as wide as the meatus. Parietal ridges not raised posterior to the postglenoid fossa. Masticator and buccinator foramina joined in a narrow, horizontal slit or a large oval foramen (MCZ 37964) (fig. 8B). Posterior opening of the alisphenoid canal thin walled and opens in a tube beneath the strut (pterygoid plate) between the pterygoid canal and the foramen ovale (fig. 8A); it sometimes lacks the dorsal wall and appears absent. There are no sphenopalatine vacuities. Auditory bullae not inflated, nearly flat in lateral profile, and markedly smaller than those of most other echimyines (figs. 7D, 8B); meatus rim pointed outward. Postglenoid foramen slitlike
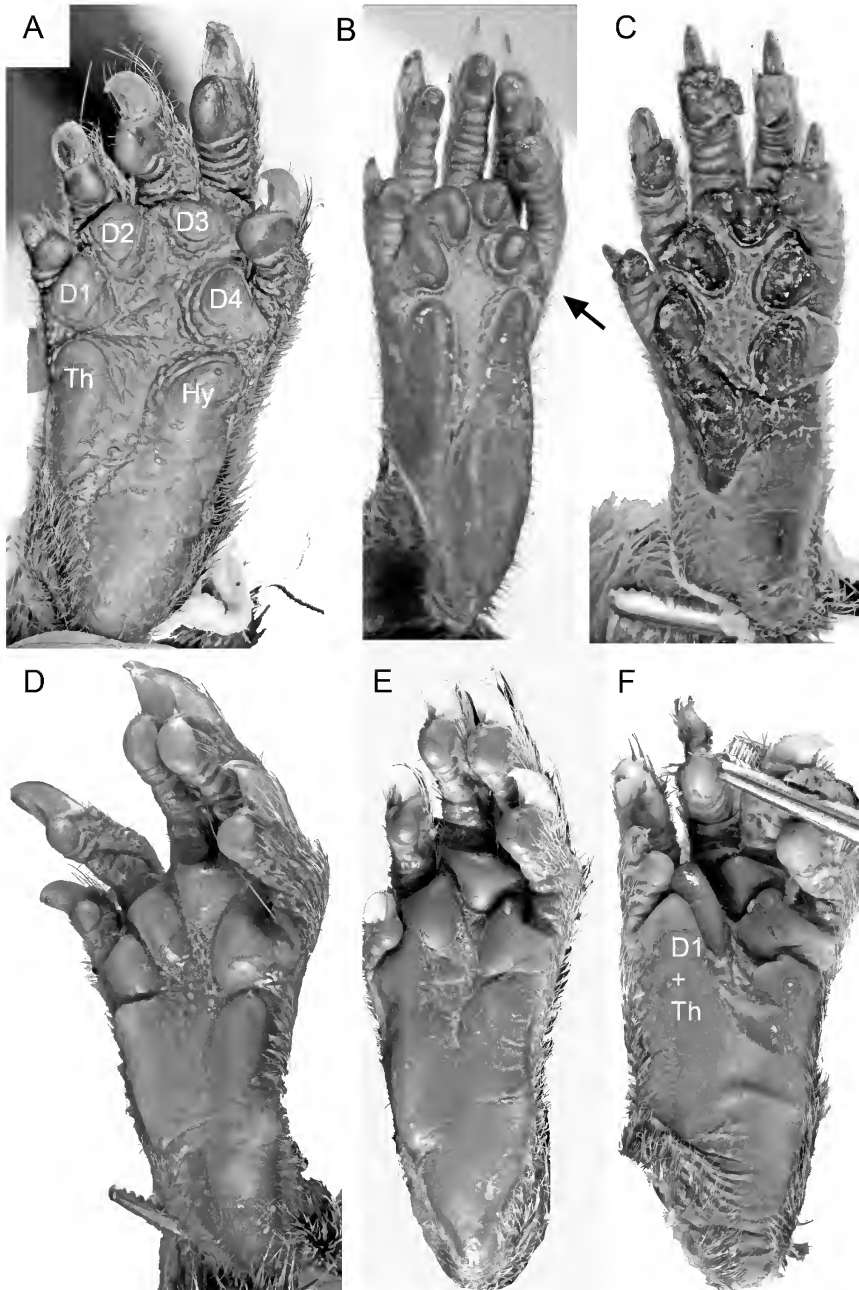
FIG. 6. Variation among genera in plantar surfaces of hindfeet, fluid-preserved specimens. **A,** *Toromys rhipidurus* AMNH 276710; **B,** *Pattonomys carrikeri* USNM 496501; **C,** *Phyllomys pattoni,* UFES 121; **D,** *Makalata cf. didelphoides* USNM 581981 (Bolivia); **E,** *M.* cf. *macrura* USNM 496480 (Venezuela); **F,** *Echimys chrysurus,* USNM 549839 (Rio Xingu). Note small digital pads, especially D3, and collars of small tubercles around pads in (A–C); large digital pads and no collars of tubercles in (D–F); merged D1 and thenar pad in (E–F), leaving three separated digital pads; and differences in digital pad shapes (see text). Abbreviations: **D,** digital pads; **Th,** thenar pad; **Hy,** hypothenar pad. Arrow in A indicates supernumerary separated pad of *Pattonomys* spp. Figures not to scale. Photo panel C, Yuri Leite.
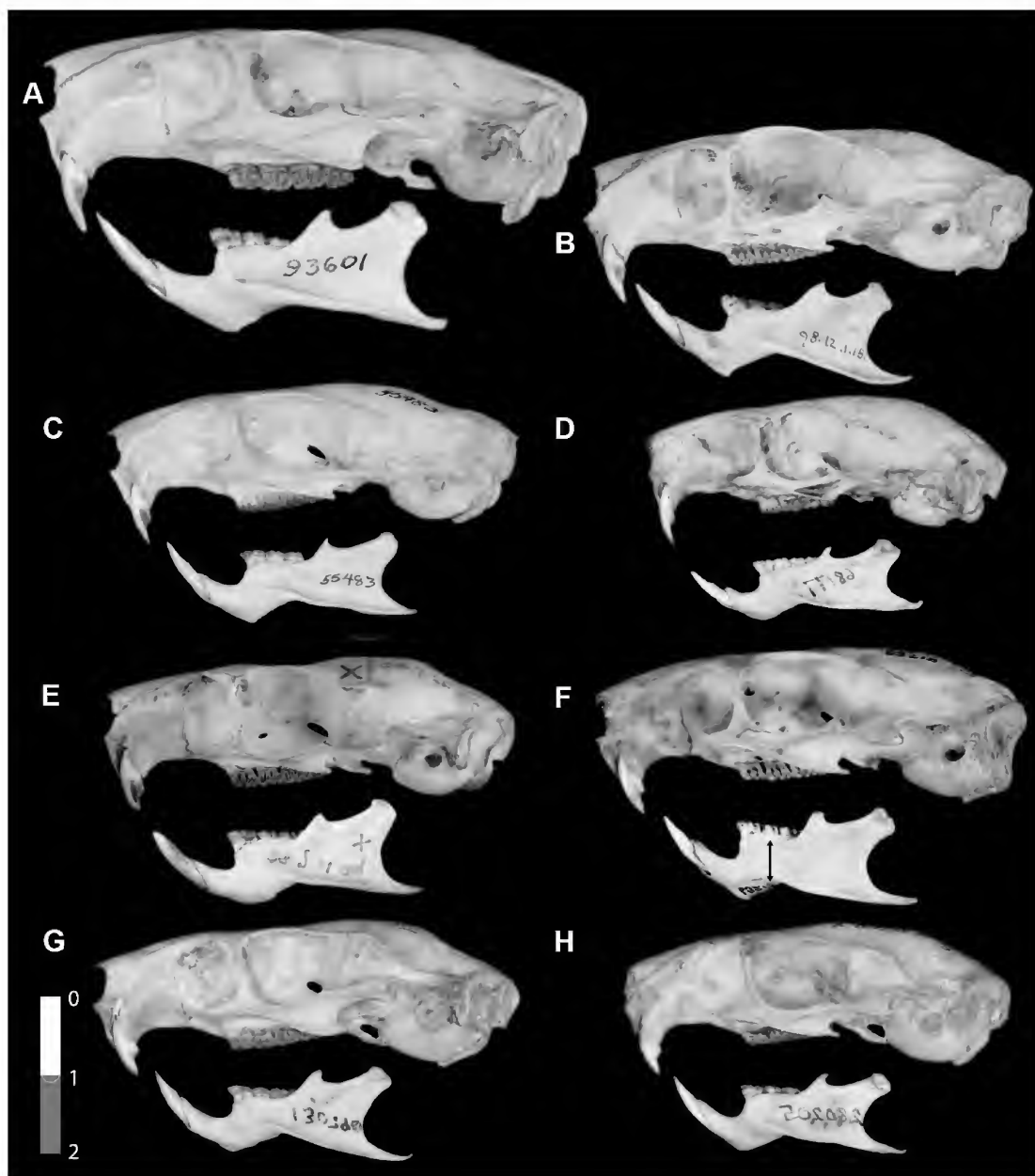
FIG. 7. Crania and mandibles, lateral view. **A,** *Toromys grandis* AMNH 93601; **B,** *T. rhipidurus* BMNH 28.7.21.89 (holotype); **C,** *T.* sp. nov., FMNH 55483 (holotype), **D,** *Leiuromys occasius.* AMNH 71897; **E,** *Pattonomys punctatus* BMNH 98.12.1.18 (holotype); **F,** *P. flavidus* USNM 63218 (holotype); **G,** *P. carrikeri* AMNH 130790; **H,** *P. semivillosus* USNM 280205. Black arrow in F indicates the deep mandible of *P. flavidus* relative to its congeners.
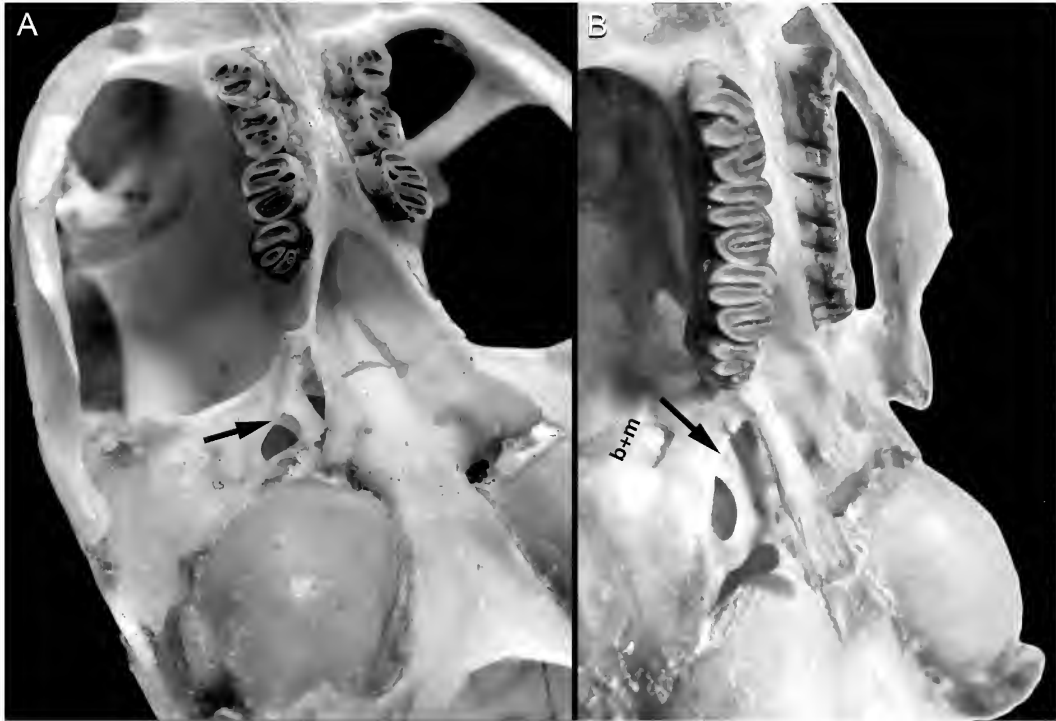
FIG. 8. *Leiuromys occasius* basicrania. **A,** internal position of posterior alisphenoid canal (arrows), MCZ 37964 (Ecuador, left M3 lacking); **B,** buccinator and masticatory foramina joined in a slit (b+M) FMNH 84427 (Peru). Note absence of inferior jugal process, shallow or absent grooves and ridge on anterior palate between premolars, and small tympanic bulla in B.

and enclosed below by a crest of petrosal. The ridges and grooves posterior to the end of the incisive foramina terminate anterior to the premolars, with shallow or absent extensions onto the palate between the toothrows (fig. 8A, B). Viewed dorsally, the interparietal is an even-width, narrow strip bowed smoothly posteriorly at the parietal suture (fig. 9D). Coronoid process of the mandible slender and recurved, above a shallow sigmoid notch (fig. 7D). Masseteric crest strongly developed and curved upward anteriorly for about half the width of the mandible; spine of the condyloid ridge on the interior of the mandible does not extend much more than halfway up the condyloid process, except on a specimen from southern Peru. Maxillary toothrows short, 7.3–10.75 mm (table 6); incisors bone white; roots of the upper incisors lie outside the maxillary base of the zygoma. Lower premolar quadralophodont, comprised of a curved anteroloph and a straight metolophid that join with wear into a D-shape around a central fossettid, which joins with wear by a central mure to the lingually opening V-shaped posterior lophid pair (fig. 11B). Hypoflexids on m1 to m3 fall nearly opposite the middle of the mesolophids, such that the teeth viewed from the lingual side are nearly symmetrical, rounded M-shapes. Upper lingual and lower labial reentrant folds (hypoflexi) short and wide, about 1/4 of the width of tooth, when worn they form subcircular fossettes; labial reentrant folds are long, and of equal length (meso- and metaflexi), such that when worn to a mure in
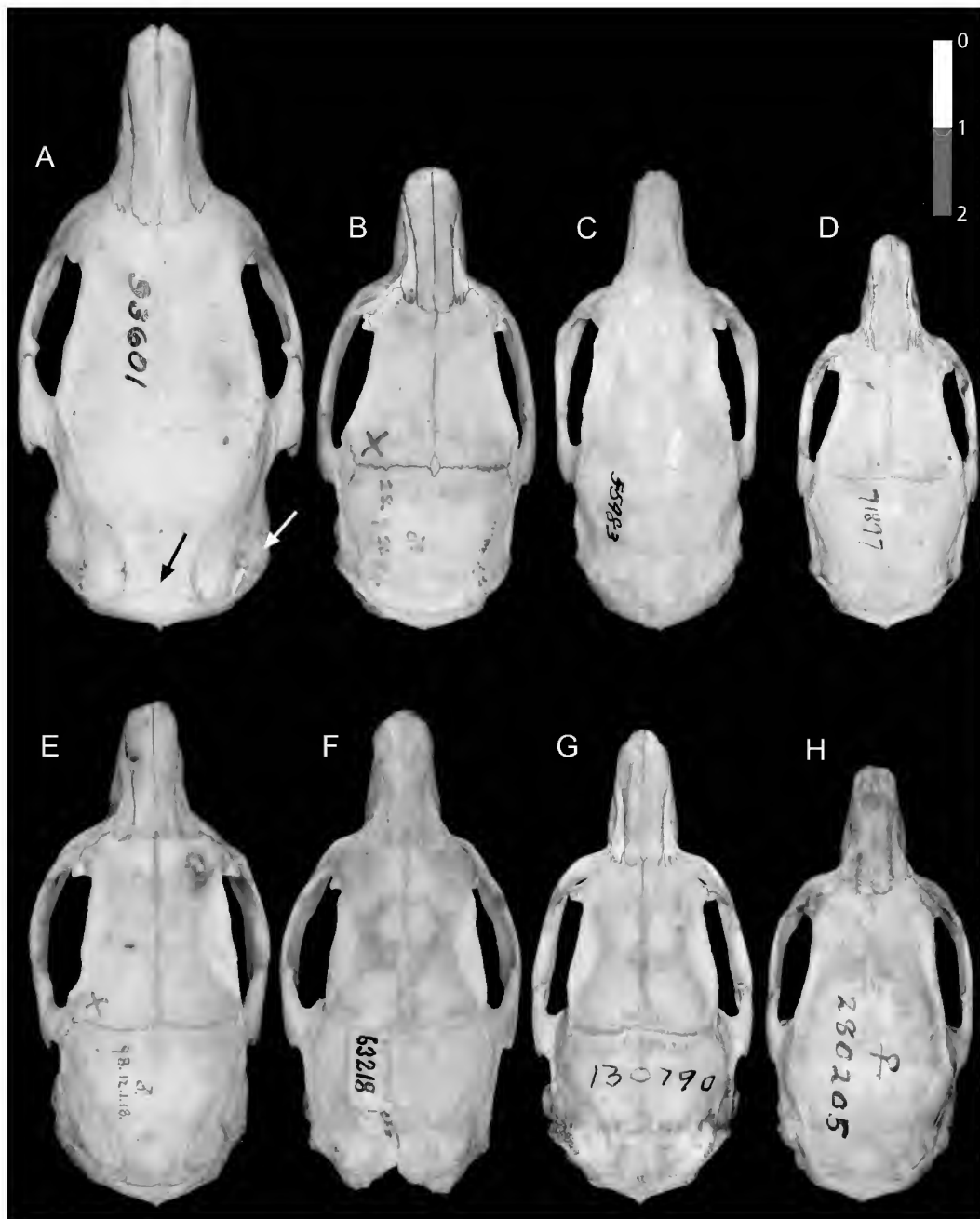
FIG. 9. Crania, dorsal view. **A,** *Toromys grandis* AMNH 93601; **B,** *T. rhipidurus* BMNH 28.7.21.89 (holotype); **C,** *T.* sp. nov., FMNH 55483 (holotype), **D,** *Leiuromys occasius.* AMNH 71897; **E,** *Pattonomys punctatus* BMNH 98.12.1.18 (holotype); **F,** *P. flavidus* USNM 63218 (holotype); **G,** *P. carrikeri* AMNH 130790; **H,** *P. semivillosus* USNM 280205. Black arrow in A indicates recurved parietal-interparietal suture, white arrow the expanded squamosal shelf.

FIG. 10. Crania, palatal view. **A,** *Toromys grandis* AMNH 93601; **B,** *T. rhipidurus* BMNH 28.7.21.89 (holotype); **C,** *T.* sp. nov., FMNH 55483 (holotype), **D,** *Leiuromys occasius.* AMNH 71897; **E,** *Pattonomys punctatus* BMNH 98.12.1.18 (holotype); **F,** *P. flavidus* USNM 63218 (holotype); **G,** *P. carrikeri* AMNH 130790; **H,** *P. semivillosus* USNM 280205.

FIG. 11. *Leiuromys occasius* upper (top row) and lower (bottom row) occlusal patterns of cheek teeth at three states of toothwear. **A,** FMNH 84427; **B,** FMNH 84259; **C,** MCZ 37964, reversed. Note the trilophodont M3, the rounded posterior edges of the lower molars, the position of the mure of M1–2 on the lingual edges of the teeth, the quadralophodont lower premolar, and the M-shaped lower molars (viewed lingually).
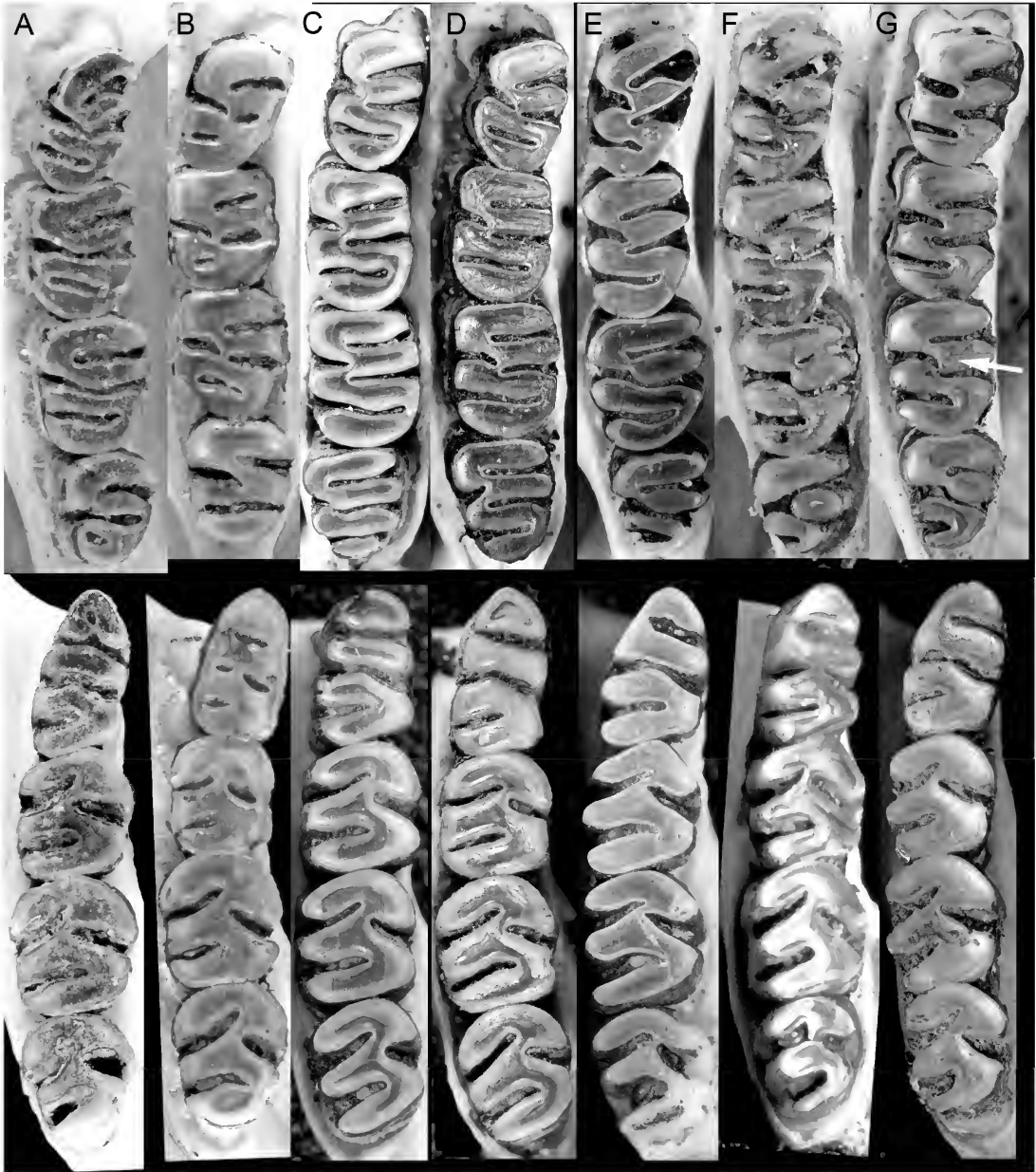
FIG. 12. Occlusal patterns of upper (top row) and lower (bottom row) toothrows of *Toromys* and *Pattonomys* species, not to scale. **A,** *Toromys* sp. nov. FMNH 55483 holotype; **B,** *T.* sp. nov. LSUMZ 8904, an old individual; **C,** *Toromys grandis* AMNH 93604; **D,** *Toromys rhipidurus* AMNH 98667; **E,** *Pattonomys carrikeri* AMNH 31530; **F,** *P. semivillosus* USNM 280205; **G,** *P. punctatus* BMNH 9812118 (holotype). In *Toromys* maxillary teeth (A–D) note laminar appearance of narrow, nearly parallel molar flexi, lophs of nearly uniform width, and mures lingually (left) of center of teeth. In *Pattonomys* (E–G) note short, offset flexi, short, wide protoloph (arrow) especially pronounced on M2, mures about in midtooth; unequal loph sizes give irregular appearance. On mandibular teeth, note the straight (flat) posterior molar edges; the square (flat) lingual edge of central lophid (entoconid) in *Toromys* (A–D, also compare with fig. 17).

FIG. 13. Head colors of specimens. **A,** *Toromys,* sp. nov. LSUMZ 8904; **B,** *Toromys rhipidurus* FMNH 87248; **C,** *Makalata* cf. *macrura* LSUMZ 14408. Specimens in panels A and C were collected at Yarinacocha (type locality of *Toromys,* sp. nov.). The tip of the muzzle is variably buff to rusty in *Toromys* sp. nov. (fig. 16), while *Makalata* from some distant populations are not as bright rusty as A. On *Makalata*, the rust color extends well behind the eye above and below. Also note the coarser, more robust vibrissae of both *Toromys*, the more developed fringe of salient wispy hair on rim of the *Makalata* ear (also typical of *Pattonomys* spp.), and the less robust claws of *T.* sp. nov. compared to those of *T. rhipidurus*.

M1 and M2, the mure is on the far lingual edge of the tooth (fig. 11B). Mandibular cheekteeth all with curved posterior borders. M3 trilophodont in all specimens examined, with the third loph much reduced (fig. 11C). Worn lower molars nearly circular, somewhat resembling those of *Isothrix* (fig. 11C).

COMPARISONS WITH OTHER GENERA: *Leiuromys* is most easily confused externally with the distantly related taxa *Mesomys* species and *Phyllomys pattoni*. Species of *Mesomys* all have conspicuously hairy tails with brown, outward-curling hairs and a slight-to-prominent pencil-like tapering at tip (Patton et al., 2000). In *Mesomys* the buff or whitish ventral pelage field is sharply demarcated from the spiny dorsal pelage. The molar occlusal pattern has flexi/flexids compressed into narrow parallel lines that do not open on sides of the teeth. *Phyllomys pattoni* have rusty-tipped spines and rusty sides, and an occlusal pattern of separate laminae (Emmons et al., 2002). *Pattonomys* species are larger, with grizzled gray heads, sides, and feet, white lower cheeks and throat, a fuzzy tail, and a distinct molar occlusal pattern, including straight poste-rior edges of the lower cheekteeth (fig. 12E–G). The spines of *Pattonomys* species taper more sharply at the tips (fig. 4B). *Makalata* species have tails slightly but distinctly hairy, with banded tail hairs, and short, rectangular tail scales in even rings (fig. 5D); a uniformly ochraceous- or reddish-agouti pelage of dusky and yellowish; multibanded, spinous aristiform hairs with short, pale, hairlike tips that are not as wide or sharp as in *Leiuromys* (fig. 4C); rostra that are reddish anteriorly to above and behind the eyes (fig. 13C), and rusty pelage around the tail base. *Phyl-lomys* species and *Echimys chrysurus* have one inguinal and three lateral pairs of mammae, whereas the other genera have two lateral pairs, and if present, inguinal mammae seem obsolete (unused in parous females). All other Echimyini usually have a quadralophodont M3, but *P. semivillosus* can lack the fourth loph. In *Makalata* the lower premolars are pentalophodont (illustrated in Emmons, 2005). The lower premolar hypoconid is a rounded point in genera of the *Echimys* clade, while it is flat in *Pattonomys* and *Toromys*; in the latter often slightly indented (Iack-Ximenez et al., 2005: fig. 11).

Leiuromys occasius (Thomas, 1921)

Echimys occasius Thomas, 1921: 450 (original description).
Echimys armatus occasius: Ellerman, 1940: 112 (name combination).
Makalata occasius: Emmons and Feer, 1997: 237 (name combination).
Pattonomys occasius: Emmons, 2005: 282 (name combination).

TYPE SPECIMEN: The holotype, BMNH 21.2.15.6, consisting of the skin and skull of a juvenile female (with M2 unerupted), was collected for Ludovic Söderström (probably by his native employees; see Chapman, 1926) on 20 February 1914, and subsequently acquired by exchange from the Stockholm Museum.

TYPE LOCALITY: Allegedly "Gualea, Ecuador, west of Pichincha. Alt. 4000 [ft]" (Thomas, 1921: 450). Tate (1935: 435) wrote "(Erroneous?)" next to this locality, and Emmons (2005) likewise surmised this type locality to be erroneous, because Gualea is in the western foothills of the Andes and all other known specimens are from lowland evergreen forests of eastern Ecuador and Peru. Moreover, the microhabitat noted on the skin tag is not plausible.[3] In 1914 Söderström acquired birds from around Pichincha, Gualea, on the western Andean slope, but also a montane hummingbird (*Aglaiocercus kingii*) from Baeza (VertNet records) at 1900 m in the foothills of the eastern Andes. Baeza is only about 30 km from Río Suno Abajo, and 60–70 km from Río Jatunyacu (800 m), both collection localities of *L. occasius*. A Söderström specimen of a motmot species known from Baeza (now *Momotus momotus*) was likewise erroneously labeled as from Gualea (Chapman, 1926: 273). Therefore, the type locality (defined as the locality where the holotype was actually collected; ICZN, 1999) is almost certainly somewhere in the lowlands of eastern Ecuador.

DIAGNOSIS AND DESCRIPTION: As for genus (above).

HABITAT: All examined specimens except the holotype are from 150 to 800 m in regions of tall, evergreen, humid Amazonian forests within about 300 km of the Andean foothills. All such collection localities are along rivers (the main travel routes when they were collected), and the collectors did not record habitat details. One of us (LHE) in 1982 photographed a *Leiuromys*, provisionally identified by its bright orange-buff underparts, gray cheeks, naked tail, and white teeth, at Cocha Cashu Biological station in Manu National Park (fig. 1, locality 32). It was in whitewater floodplain forest, sitting motionless crosswise on a wide branch in the under canopy, at about 8–10 m height. No other Echimyini are known from the region of the southern population in the Department of Madre de Dios, Peru (Emmons et al., 2015a: maps 494–498), where there is a mysterious distribution gap for *Makalata* and *Isothrix*, no *Echimys*, and the only known arboreal Echimyidae are *Dactylomys boliviensis* and *Mesomys hispidus*.

REMARKS: The two groups of northern (Ecuadorean) and southern (Peruvian) specimen localities are over 1000 km apart. A sequenced individual from each population (FMNH 14409, MCZ 37964) showed a *cyt-b* sequence divergence of 2% (table 2), a difference that merits further investigation. Because only three specimens are recorded from southern Peru, and three of the nine specimens that we examined are subadults with unerupted M3, we did not try to

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[3] "Killed between the stones in a stream" is written on the label, but this was not mentioned by Thomas (1921).

FIG. 14. Living *Toromys* and *Pattonomys*. **A,** *Toromys grandis*, lower Rio Purus, (fig. 1, locality 31). Note the elongate body, the longer black hair on the proximal tail, and the broad foot with narrow heel. There is a post-auricular patch of pale skin. The anterior bright eyeshine spot seems to show an oval, vertical pupil, the other spot is a reflection of the flash (image by Vinicius Carvalho). **B,** *Pattonomys semivillosus* in a black mangrove tree (*Avicennia germinans*) in Parque Nacional Isla de Salamanca, Magdalena, Colombia. The white postauricular tufts above and behind the ear are striking (photograph by Fabrice Schmitt). **C,** *Toromys rhipidurus*, captured near Iquitos, Peru. The evident cream-colored postauricular patches are not visible on most museum skins. The camera-flash has accentuated the yellow midbody hues (image by Pamela Sánchez-Vendizú).

test for morphological variation between the two populations, but specimens from southern Peru seem to have paler underparts, with more self-white areas, than specimens from Ecuador and northern Peru.

SPECIMENS EXAMINED: ECUADOR: *Pichincha*, Gualea, 4000′ (BMNH 21.2.15.6 [holotype]); *Napo*, Río Suno abajo 800 m (AMNH 68177); "Napo" (BMNH 34.9.10.202); Río Jatún Yacu (= Jatunyacu), 750 and 800 m (MCZ 37964*). PERU: *Loreto*, Maynas, Boca Río Curaray (AMNH 71897); Boca Río Santiago (AMNH 98262); *Madre de Dios*, Río Colorado, near the mouth (FMNH 84259*, 84427).

Pattonomys Emmons, 2005

TYPE SPECIES: *Nelomys semivillosus* I. Geoffroy St.-Hilaire, 1838.

CONTENTS: Four valid species, as diagnosed below.

DIAGNOSIS: A genus of large, arboreally adapted Echimyidae (tables 5, 6). Dorsal pelage with strong, wide, gray-based aristiform spines that narrow to sharp tips; some spines entirely black or dusky tipped, others with dark subterminal bands and contrasting white tips that impart a pronounced speckled appearance (fig. 4B). Prominent pale postauricular patches (fig. 14B). Cranium generally like that of *Makalata* and *Echimys,* short and broad, with more or less expanded, winglike supraorbital shelves that curve upward from the frontal bones (figs. 7E–H, 9E–H, 10E–H; see also Emmons, 2005: figs. 11, 14). Upper cheekteeth with widely open flexi, greatly anteroposteriorly expanded protocone and posteroloph (probably metaloph and posteroloph combined), and a markedly oblique paraflexus on dP4 (fig. 12E–G). These expanded lophs are accentuated with wear. The four lophs of dP4–M2 are markedly unequal in length and width: the anteroloph is broad and squared lingually, tapering labially; and the posteroloph is pointed labially and strongly curved along the posterior margin of the tooth. Lower premolar tetralophodont, with two labial and two lingual flexids (fig. 12E–G).

DESCRIPTION: Spines wide, sharp, and stiff, with tips not drawn out into long hairlike processes but end in microscopic hairs (fig. 4B). White-tipped spines are sprinkled singly among the lateral and dorsal pelage from shoulder or midback to rump, increasing posteriorly in number and in the length of pale tips. Pale-tipped spines sparsely and evenly distributed over the speckled rump. Dorsal spines mixed with fine, ochraceous yellow to orange setiform bristles and sparse dull reddish or yellow-ochraceous underhairs; pelage slate-gray based. Head, neck, and shoulders grizzled gray lined with black, in a mixture of long, narrow, dusky and whitish aristiforms (fig. 14B). Sides grayish from head to flank between gradually or sharply demarcated pale venter and yellowish or reddish-brown tinged middorsal pelage. Ear tips with an inconspicuous, sparse fringe of long fine, salient hairs. Dorsal pelage extends onto the tail base to about the hind feet of study skins; distal tail evenly covered above and below to its tip with fine, monocolored white to red-brown hairs that do not cover scales but curl outward, so that the tail looks distinctly hairy (fig. 5A). Vibrissae robust, dense, and black, the longest reaching to shoulder when laid back. Two pairs of lateral mammae lie in the dorsal pelage field, one about midway between the limbs, the other

FIG. 15. *Pattonomys* basicrania. **A,** *Pattonomys punctatus* USNM 374741; **B,** *P. carrikeri* USNM 456429. Note separate masticatory and buccinator foramina (arrows), robust extra bony rings below meatus, wide mesoptery-goid fossa, and less inflated auditory tympanic bullae in A; joined foramina and more inflated bullae in B.

just anterior to the flank. Hind feet, based only on *P. carrikeri,* with four small, ovoid digital pads and a fifth small outer pad budding laterally from D4. Hypothenar pad joined to large naked heel pad with only a slight depression between them (fig. 6B); thenar pad elongate and slender, separated from the joined hypothenar and heel pads by a deep, narrow groove containing palmar tubercles. Plantar surfaces between pads with a few inconspicuous tuber-cles; digital pads bordered by distinct rings or collars of tubercles (fig. 6B); forefoot digital pads also bordered by indistinct collars of tubercles, but the central palm with few or none. On the cranium, the frontal-squamosal suture at the back of the orbit is raised in a sharp ridge (fig. 7E–H). Mastoid processes short, to the middle or lower edge of the auditory meatus, adpressed to the bulla, and enclosed to the tip by occipital bone (fig. 7E–H) and see also Emmons (2005: 263, fig. 5). Postglenoid foramen enclosed below by the petrosal bone in an anteriorly facing tube; the salient ventral lip of the auditory meatus is usually visible in dorsal aspect (fig. 9G), and is further extended in mature individuals by two overlapping additional bony rings that cup the meatus ventrally and laterally, but are incomplete dorsally (fig. 15A). These are not fused and can be lost in skin preparation. Nasal bones in dorsal aspect flared distally, slightly pinched in medially, and about squared or slightly rounded posteriorly (fig. 9E–H). Incisive foramina small, narrow, and slightly ovoid, with deep grooves and ridges leading onto the anterior palate to between the first or second cheekteeth (fig. 10E–H). Maxillary toothrows nearly parallel. Mandible with a low coronoid process only slightly shorter than the narrow condyloid process, and a shallow sigmoid notch (fig. 7E–H). Mandibular foramen in a fossa arising low on the condyloid ridge; masseteric crest

not curved upward anteriorly, but forms a nearly straight line from the base of the angular process (fig. 7E–H). Incisor enamel yellowish white, lowers tinged more orange than uppers; upper incisors opisthodont, robust, and strongly curved, with the base of the roots outside of, or level with, the maxillary base of the zygoma. Maxillary cheekteeth (fig. 12E–G) squarish to rectangular, with rounded posterior lophs and an uneven appearance due to unequal loph sizes. DP4–M3 always with two labial and two lingual flexi. Anterior lingual flexi (paraflexi) short, reaching only about half of the width of the tooth; the posterior lingual flexi (hypoflexi) longer; both labial flexi (para + hypoflexi) extend slightly more than half of the width of the tooth and are of the same length. DP4 and M1 always with a mure in the center of the tooth; M2–3 are with or without a mure, and all four flexi slant posteriorly from the edge to the middle of the tooth, so that labial and lingual flexi slant slightly in opposite directions. If without a mure, the joined flexi have a sharp elbow where the mure would be (fig. 12G, arrow). Lower premolar usually divided by one central flexid into two V-shaped lophs, but with wear forms a midtooth mure. In m1–2 the lingual flexids are parallel and of about equal length. Flexids of all mandibular cheekteeth wide. Hypoconid with a flat labial profile (fig. 12E–G). Posterior borders of lower cheekteeth straight. Phallus of *P. carrikeri* long and slender, with a long, pointed, bacular papilla, small urethral lappet, border of ventral crater wall a straight line without a U- or V-shaped ventral fold (Emmons, 2005: fig. 10C); those of other species are undescribed. Karyotypes of four specimens, which from their localities we assign to *P. flavidus* and *P. carrikeri*, were identical, $2N = 94$, among the highest found in Mammalia (Aguilera et al., 1998).

Comparisons with other genera: A white-speckled, spiny pelage is unique to the genus, although *Leiuromys*, *Mesomys*, *Lonchothrix*, and *Phyllomys pattoni* have strong, buff-tipped spines. There is no geographic overlap of these genera with *Pattonomys*. The maxillary occlusal pattern of *Pattonomys* species is unique for the family, and even single or worn upper teeth usually can be identified to genus. A quadralophodont lower premolar is shared only with *Leiuromys* among Echimyini, but in that genus, the mure is near the lingual edge of the upper molars, and the posterior edges of the lower cheekteeth are curved, while the mure of *Pattonomys* species is near the center of the upper molars, and the posterior edges of the lower molars are straight. The flexids of *Pattonomys* are wider than those of other Echimyini. Likewise, the long, thin, simple phallus of *P. carrikeri* is thus far unique among the Echimyini; those known for the other genera are short, thick, and with additional folds (Leite, 2003; Emmons et al., 2005: fig. 10C), but descriptions are needed for other species in every genus.

Pattonomys semivillosus (I. Geoffroy St.-Hilaire, 1838)

Nelomys semivillosus I. Geoffroy St.-Hilaire 1838: 887 (original description).

Type specimen and type locality: Geoffroy St.-Hilaire (1838) examined three specimens sent to de Blainville and Roulin from Cartagena by the French consul, M. Pavageau. One syntype is known (MNHN-ZM-MO-1995-1397, C. Callou, personal commun), an adult skull without mandible and A-7672 written on the cranium, original no. 408b). The original external

measurements (body and tail each 195 cm) cannot be associated with the syntype skull; "Carthagène, (Nouvelle-Grenade)," Cartagena, Bolívar, Colombia.[4]

DIAGNOSIS AND DESCRIPTION: The smallest (tables 5, 6) and most heavily spined member of the genus. Upperparts generally gray with middorsum tinged brown; back and sides sprinkled with white-tipped spines posteriorly from neck; rump densely spiny and white speckled (figs. 4B, 14B). Head grizzled gray above, heavily lined with black, with prominent white postauricular patches visible above the rims of the ears, and narrow dusky eye rings (fig. 14B). Muzzle, cheeks, and throat white or cream. Underparts sharply demarcated white or tinged pinkish buff, colored especially behind the forelegs and in the inguinal region. Dorsal aristiforms wide, strong, and sharp, with blackish subterminal bands and dark or white tips. Dorsal underhairs ochraceous yellow to slightly reddish. Distal tail hairs brown. Hind foot of a dried skin is like those of *P. carrikeri* (fig. 6B), with six well-separated pads, a supplementary lateral pad, and the space between pads filled with small tubercles. Skull is lightly built for the genus, with supraorbital shelves not greatly expanded or curved upward. Inferior jugal processes slender and delicate. Upper incisors slightly opisthodont (fig. 7H). Buccinator and masticatory foramina separate (fig. 15A). Palatal notch (mesopterygoid fossa) narrow and straight sided, bordering a narrow opening. Teeth as for genus.

GEOGRAPHIC RANGE AND HABITAT: Known only from northern Colombia (fig. 1), in the basin of the lower Río Magdalena and its tributaries, where it has been collected in forested swampy areas (locally known as *ciénagas*). In Isla de Salamanca National Park it occurs in mangrove forest (fig. 14B).

SPECIMENS EXAMINED: COLOMBIA: *Bolívar*, Cartagena, (MNHN-ZM-MO-1995-1397 [holotype]); *César*, Valledupar, Río Guaimaral, (USNM 280204*); Valledupar, El Orinoco, (USNM 28205, 28206, 38207, 280208); *Magdalena*; Atlántico, lower Río Magdalena, opposite Barranquilla, (FMNH 69117, 69118*).

Pattonomys punctatus (Thomas, 1899)

Loncheres punctatus Thomas 1899: 153 (original description).

TYPE SPECIMEN AND TYPE LOCALITY: The holotype (by original designation, BMNH 98.12.1.18), an adult male skin and skull, one of three specimens collected 2 July 1898 by G.K. and S.M. Cherrie, at "Caicara, Orinoco," Bolívar, Venezuela.

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[4] In the 1830s de Blainville chaired Natural History and Anatomy at MNHN, and I. Geoffroy St.-Hilaire noted that he owed de Blainville and Roulin for "communication" of the specimens to him (1838: 887). He later added that those specimens were poorly preserved and half putrified, but that afterward he received another in good condition (presumably after describing the species) from which he redescribed it in much greater detail (1840: 422). Cécile Callou (MNHN) has kindly researched the history and provenence of MNHN-ZM-MO-1995-1397, which when examined in 1999 by L.H.E. was labeled A-7276 (an 1850 catalog number) and two other numbers. It has now been recataloged as a syntype, with a new number (C. Callou, personal commun.).

DIAGNOSIS AND DESCRIPTION: The largest species of the genus in nearly all measurements (tables 5, 6). Head grizzled gray, a mixture of black finely streaked with white, with large whitish postauricular patches. Pelage of back pale gray-based, yellowish agouti streaked with black, with rusty tints on posterior middorsum, rear of rump slightly darker than midback. Black-banded, white-tipped aristiforms on rump only (two specimens from Apure), or a few also on midback (the holotype and a specimen from Bolívar); fine underhairs rusty. Sides of head and shoulders, and tops of feet, grizzled gray. Underparts sharply demarcated pale gray or white with pale buff on anterior and inguinal areas; inner limbs white. Tail clothed distally with fine dusky hairs, slightly paler below. Cranium robust, with wide, strongly developed supraorbital shelves angled upward and raised above the frontals in old individuals; parietal crest strongly developed. Zygomatic arches strongly bowed outward in dorsal view (fig. 9E). Jugal robust and dorsoventrally deep. Upper incisors orthodont (fig. 7E). Masticatory and buccinator foramina separate (fig. 15A). Palatal notch wider than in other congeners, with outwardly bowed sides bordering a wide canal. Molar rows slightly diverge posteriorly to accommodate the wider mesopterygoid fossa (fig. 10E). Palate wide, about as wide as the molars between the roots of M1. Incisive foramina narrow and parallel sided. Auditory tympanic bullae not inflated, the lateral profile of the anterior bulla nearly flat (fig. 7E).

GEOGRAPHIC RANGE AND HABITAT: Known only from Venezuela near the Rio Orinoco and its tributaries in Apure and Bolívar states. Perhaps from gallery forests, as the localities are near rivers in regions generally of seasonally flooded grassland (*llanos*).

SPECIMENS EXAMINED: VENEZUELA: *Bolívar*, Caicara, Río Orinoco (BMNH 98.12.1.18 [holotype]), 95.12.1.20, 52.12.3.21, 93.12.1.19; AMNH 171389, 171391, 171392, 29872*, 29873); Hato La Florida, 35 km ESE Caicara (USNM 406402); *Apure*, 38 km NNW Puerto Paez, Río Cinaruco (USNM 374741, 374742*).

Pattonomys carrikeri (J.A. Allen, 1911)

Loncheres carrikeri J.A. Allen, 1911: 251 (original description).

TYPE SPECIMEN AND TYPE LOCALITY: The holotype (by original designation, AMNH 31530) consists of the skin and skull of an adult female collected by M.A. Carriker, Jr., on 15 November 1910 at "San Esteban," Carabobo, Venezuela.

DIAGNOSIS AND DESCRIPTION: Similar externally to *Pattonomys punctatus*, but smaller and upperparts usually paler and laterally more yellowish tinged (tables 5, 6); dorsal midbody between limbs washed dull rusty from long, rust-orange tipped setiforms among the spines. Scattered white-tipped aristiforms start to appear behind the shoulder and increase posteriorly. Underparts whitish gray either sharply demarcated from sides, or grading gradually, with hairs pale gray based and white tipped; midline, chest, and inguinal area nearly white. Head in front of ears, forelimbs, and tops of feet grizzled slate gray, frosted with white-tipped hairs. Postauricular pale patches inconspicuous, gray. Tail hairs blackish above, paler below. We examined the feet of fluid-fixed specimens of this species only ($N = 16$): hind feet with small, indistinct plantar tubercles between the pads; digital pads 1 and 2 elongate, narrow ovals or semicircles; a small auxiliary pad lateral to digital pad 4 always

present (fig. 6B). Incisors white and slightly opisthodont; maxillary molar toothrows straight and parallel. Cranium moderately robust, with zygomatic arches usually bowed outward. Supraorbital shelves wide and curved upward. Unique in the genus, basicranium with a single, joined masticatory and buccinator foramen (fig. 15B). Palatal notch narrow, with straight sides and a narrow canal. Auditory tympanic bullae distinctly inflated and rounded anteroventrally (figs. 7G, 10G).

GEOGRAPHIC RANGE AND HABITAT: Northern Venezuelan lowlands (fig. 1) from about Apure and Falcón east to Caracas and south to Guárico (Zaraza). Collected in trees and from tree hollows near water sources, usually in thorn forest or isolated trees in savanna; in a general region of savannas, arid scrub, and cactus (Allen, 1911; Tate, 1935; Handley, 1976).

REMARKS: This species is represented by many specimens in collections, and there is much variation in color pattern of the underparts within series of specimens from the same locality. The original description states it to be much darker than *P. punctatus*, with blackish middorsum, but this coloration does not seem to be found in specimens seen by us. However, Allen (1911), as we did, noted the more inflated bullae and markedly narrower palatal notch ("posterior nares") of *P. carrikeri* compared to those of *P. punctatus*. We have not dissected the basicranial region and what we call the "joined" maxillary and buccinator foramina is present as a single wide foramen positioned laterally at the site of the buccinator (fig. 15B). We follow the nomenclature of Wahlert (1974: 370, fig. 1) in classing them as joined, but instead the masticatory foramen may simply be lacking and the associated artery passed internally through the alisphenoid canal.

SPECIMENS EXAMINED: VENEZUELA: *Carabobo*, San Esteban (AMNH 31530); Montalbán, 1.2 km SE Montalbán, El Castaño, (USNM 442715); *Falcón*, Urama, 19 km NW Urama, km 40, (USNM 372701); *Lara*, Río Tocuyo, (AMNH 130790–130814, 131087); 10 km N El Tocuyo, Caseria Boro, (USNM 456429, 456430, 456433–456437, 456439, 456440, 456443, 456444*, 496483, 496485, 496487–496490, 496492, 496494–496496, 496500–496506, 496508, 496509); San Miguel, San Gerónimo, (AMNH 132836–132844, 132846); San Miguel, Hacienda La Fortuna, (AMNH 132849–132859); San Rafael (AMNH 132845, 132847); *Distrito Federal*, Caracas, (AMNH 130815); *Guárico*, Zaraza, (AMNH 135442, 135443, 135471, USNM 314996); Río Orituco, 10 km W of Chaguaramas, (ROM 107955*).

Pattonomys flavidus (Hollister, 1914)

Loncheres flavidus Hollister 1914: 143 (original description).

TYPE SPECIMEN AND TYPE LOCALITY: The holotype (by original designation, USNM 63218) consists of the skin and skull of an adult male with shot damage to the head, collected by W. Robinson on 9 July 1895 at "El Valle, Margarita Island," Nueva Esparta, Venezuela.

DIAGNOSIS: Perhaps as large as *Pattonomys punctatus*, cranium intermediate in size between *P. punctatus* and *P. carrikeri* (based on one individual, tables 5, 6). Dorsal pelage grizzled ochraceous yellowish lined with black, slightly browner over the rump. White-tipped spines robust and confined to the rump. Underhairs ochraceous yellow. Head and neck grayish; underparts yellow-buff. The postauricular patches seem gray-white, but head skin badly damaged. Feet gray above. Cranium with zygomatic arches tapering anteriorly, not bowed outward; mastica-

tory and buccinator foramina separate. Palatal notch V-shaped, with straight borders; bullae not inflated (9F, 10F). Mandible robust and deep below the toothrow (fig. 7F: arrow).

REMARKS: Based on the holotype, *Pattonomys flavidus* is not more clearly aligned in morphology with any one of the other three species. We failed to obtain good mitochondrial sequences for *P. flavidus*, however, some 100 bp Illumina reads indicate a close relationship to its geographical neighbor *P. carrikeri* (sequences identical), but with insufficient data to place it definitively, so we provisionally maintain it as an independent lineage. This island endemic is apparently represented in collections only by the 1895 type specimen. Three recent specimens were karyotyped, but not preserved (Aguilera et al., 1998). Nonetheless, they prove that the species was extant in the mid-1990s.

GEOGRAPHIC RANGE AND HABITAT: The type locality is El Valle, on the eastern end of Margarita Island, Venezuela, but recent specimens were from the Macanao Peninsula at the western end of that island (Aguilera et al., 1998). The lowlands of the island are largely deforested, but there is a forested protected area on the western side, where the recent specimens were captured, and the highlands of the eastern side, the provenance of the holotype, remain patchily forested (Google Earth, 2017). This continental-shelf island is separated from the mainland by two shallow (<10 m deep), open-water channels (9 km, 10 km) and it would have been connected to the mainland during glacial periods as recent as 8000 y.b.p. (Guilderson et al., 2000). Two specimens were captured by hand from tree holes (Aguilera et al., 1998).

SPECIMENS EXAMINED: VENEZUELA: *Nueva Esparta*, Margarita Island, El Valle (USNM 63218* [holotype]).

Toromys Iack-Ximenes et al., 2005

TYPE SPECIES: *Loncheres grandis* Wagner, 1845.

CONTENTS: Three species, including a new species from eastern Peru (described below).

REVISED DIAGNOSIS: Large, arboreally adapted rats with long backs, short legs, and broad feet (figs. 6A, 14A). Tails slightly shorter than head and body length. Pelage with dorsal aristiforms of narrow, stiff, flexible bristles banded black and yellow, buff, or rusty; crown brown agouti or black; rust color, if present on the rostrum, does not extend above or posterior to the eyes from the muzzle or cheeks (figs. 13A, B; 14A, C). Tail hairs distal to the basal extension of the dorsal pelage are longest dorsally and proximally, where they can cover the scales, and they gradually shorten distally. Cranium narrow and elongate, with parietals elongate and interparietal long at the midpoint of the dorsal view, forming a wide band from ear to ear in dorsal view (fig. 9A–C). The nasal bones widen markedly to slightly anteriorly. Palate narrow (fig. 10A–C), the maxillary toothrows at the anterior root of M1 are closer together than the width of M1, and the maxillary toothrows are long relative to the basilar length of the cranium. Lophs and flexi of the maxillary cheekteeth approximately parallel and at right angles to the line of the toothrow; posteroflexi long, hypoflexi short, and the lophs are of about equal width throughout their lengths. When present, M1–M2 mures are about a third of the way in from the lingual edges of the teeth. Posterior borders of the mandibular cheekteeth nearly straight, with entoconids nearly rectangular, with square lingual edges (fig. 12A–D).

REVISED DESCRIPTION: Pelage with dorsal aristiform hair tips blunt or drawn out into long hairlike processes, not sharp spines (fig. 4D–F), the fur rubbed backward is stiff rather than spiny. If present, wider, more spinelike aristiforms have whiplike tips. Dorsal pelage extends onto the tail base to about the level of the specimen heel; tail pelage abruptly changes to long, straight, unicolor, black or brown hair that can nearly cover the scales either throughout the tail to its tip, or thins gradually down the distal two-thirds to show the scales (fig. 5C), but in all taxa the length of the tail hairs decreases from base to tip (figs. 14A, C; 16); the tail tip lacks a pencillike tapering. Two pairs of functional lateral mammae lie high in the dorsal pelage field. Plantar surfaces of the hind feet have small prominent plantar tubercles covering the spaces between and around the pads (fig. 6A). The four digital pads are small and round or slightly triangular, widely separated, and bordered by rings of tubercles; hypothenar pad wide and long, joined to the smooth naked heel pad by a poorly marked shallow depression, separated from the broad thenar pad by a narrow tubercle-filled fold. First digital pad separated from the thenar pad (fig. 6A). Hallux short, the fleshy part not extending beyond base of the second digit. Forefeet with digital, thenar, and hypothenar pads encircled posteromedially with one or two collars of tubercles, but there are few or no small tubercles on the palm between the pads. Auditory tympanic bullae not inflated in lateral view (fig. 7A–C). Raised rim of the auditory meatus discontinuous, with a wide gap on dorsal edge. A tongue of the squamosal bone often extends into the mastoid process, which is short, adpressed, and enclosed to its tip in bone. The masticatory and buccinator foramina are separate; the posterior opening of the alisphenoid canal is robustly walled, often prominent in lateral view, and separated above the fossa of the foramen ovale (fig. 17A, B). Mandible generally with a long, shallow, sigmoid notch; coronoid process not usually recurved. Spine of the condyloid ridge on the interior of the mandible extends strongly to the top of the condyloid process. Masseteric crest salient and extends as a ridge to below the first cheektooth. Root of the upper incisor extends posteriorly to behind the base of the maxillary portion of the zygoma in adults (fig. 7A–C). Lower premolar pentalophodont, with a triangular anteroloph including a fossetid, a separate metalophid bar and a joined entoconid and posterolophid pair with lingually opening posteroflexid, giving three lingual and two labial flexids (fig. 12A–D). Hypoconid with a flat labial profile. Lophs and flexi of the maxillary cheekteeth approximately parallel and at right angles to the line of the toothrow, producing a laminar appearance; the flexi extend about 2/3 or more across the width of the cheekteeth; the hypoflexi extend about one third or less the distance across the width of tooth. Anterior joined lophs of the maxillary molars open labially, while the posterior pair open lingually, or the posteroloph is variably a separate lamina, especially in *T. grandis*. Hypoconids have squared labial edges (fig. 12A–D). Iack-Ximenez et al. (2005) described and illustrated some of these and many other characters of *T. grandis*. However, we note that not all of the characters that they recorded are stable in the specimens that we examined, nor found within other *Toromys* species.

COMPARISONS WITH OTHER GENERA: *Toromys grandis*, *T. rhipidurus*, and *T.* sp.nov. differ externally from all *Echimys, Pattonomys, Makalata,* and *Leiuromys* species by the lack of any sharp, pale-tipped spines on the dorsum. They differ from *Makalata* spp. by unicolor, long tail hairs, either thickly covering tail, as in *T. grandis*, or with longer hair that shortens toward tip on the basal third.

Toromys rhipidurus have rusty muzzles, *T.* sp. nov. much less so, if at all, but all *Toromys* lack the red facial color above or posterior to the eyes of sympatric *Makalata* species (table 3, fig. 13), although not of all allopatric *Makalata* species. Both *Pattonomys* and *Toromys* species have the plantar surfaces of the hind feet with small digital pads that are encircled by rings or collars of small tubercles. Specimens of *Makalata* and *E. chrysurus* that we examined have large digital pads lacking collars of tubercles (fig. 6D–F). The tail scales of *Makalata* species are short and wide and arranged in even, narrow rings (fig. 5D). The cranium of *Toromys* can be distinguished from sympatric *Makalata* species by a palate narrower between M1 roots than is the width of that tooth, a longer and shallower sigmoid notch of the mandible, with a coronoid process that is not recurved; short, adpressed tip of the mastoid process, and generally less inflated bullae. *Makalata* species have smaller teeth and lophs of the upper cheekteeth that are wider anteroposteriorly, more curved, and distinctly tapered labially, with a consequently much less laminar appearance than in any *Toromys*. The upper premolars of some, but not all, *Makalata* taxa tend to have both pairs of lophs opening lingually, such that there are three lingual, and one labial flexi, whereas *Toromys* have two of each.

Habitat and geography: Specimens of *Toromys* species are all from riverine forests (including *várzea* and *igapó*) along the line of the Central Amazon and the lower reaches of its tributaries. The three species replace each other geographically, with the smallest in the westernmost headwaters in Peru and the largest from the central Amazon (Rio Purus) eastward to the river mouth (fig. 1). The known range of *T. rhipidurus* is small, only about 350 km across, and that of *T.* sp. nov. is even smaller. There is a large gap between known localities of *T. grandis* in Brazil and those of *T. rhipidurus* in Peru (fig. 1). Most specimens of the genus were collected by men of the Olalla family, who acquired large numbers of all arboreal Echimyidae. Some geographic range gaps may reflect gaps in the Olalla itineraries (Wiley, 2010) rather than species absence. A few Olalla label notes state that *Toromys* were collected from tree holes ("tirado en hueco de arbol") or in traps in trees ("trampa alta"), specified in two cases as at 4 m and 5 m. The exceptionally broad feet of the two larger *Toromys* species should facilitate swimming in the *várzea* and *igapó* flooded habitats that they occupy. Throughout their range, *Toromys* species are sympatric with *Makalata macrura* and *Leiuromys occasius* (upstream) or other *Makalata* species and *Echimys chrysurus* (downstream). *Makalata* species are likewise generally restricted to floodplain, riverine, or gallery forests, as are some *Isothrix* (L.H.E., personal obs.), but the ecology of neither genus has been described. Evidence of close sympatry between *Makalata* and *T. rhipidurus* or *T.* sp. nov. is provided by examined specimens of *M. macrura* from three Peruvian localities: Nuevo San Juan on the Río Gálvez (AMNH 268269[*5]), Genaro Herrera (MUSM 23823), and Yarinacocha (LSUMZ 14408).

Toromys grandis (Wagner, 1845)

Loncheres grandis Wagner, 1845: 146 (original description).

Type specimen and type locality: NMW 920; a skin with missing distal tail and skull without rostrum, sex unknown but probably male; collected by J. Natterer (JN 167) in "Amazonstrom,"

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[5] DNA sequenced to confirm identity.

this locality given by Pelzeln (1883: 63) as "Manaqueri im Mündungsbereich des Rio Solimões," now Manaquiri (Paynter and Traylor, 1991). Pelzeln also noted, from Natterer's catalogue, that the specimen was received from Estanislao stuffed and unfortunately missing the tail tip.

DIAGNOSIS AND DESCRIPTION: The largest of the Echimyini (head and body length 275–254 mm; greatest length of skull 67–70 mm; tables 5, 6). Dorsal pelage a striking mixture of pitch black and ochraceous yellow-banded aristiform bristles that impart a golden or warm ochraceous-yellow appearance at the midbody (fig. 14A). Head, crown, and neck black speckled with a few yellow-banded hairs. Underparts gray, with dark gray-based hairs tipped with translucent cream; the inguinal region tends to be cream colored. The dorsal color grades gradually into the ventral color field. Tail robust, generally about the same as head-and-body length, thickly haired at the base above and below with an extension of dorsal pelage onto tail; tail pelage changes abruptly to long, dense, straight, pitch-black hairs that nearly cover scales and are longest near tail base to form a puff on the basal third (fig. 14A). Rare specimens have the extreme tail tip whitish, but not tufted. Hind feet broad at the base of the toes and narrow at the heel (fig. 14A); blackish above, finely speckled with yellow, with black toes; ungual tufts sparse and shorter than the robust claws; palmar surfaces are pinkish, but otherwise as described for *T. rhipidurus* (fig. 6A). Cranium narrow and elongate in dorsal view, with a narrow rostrum, nasals distally flared laterally and slightly pinched-in medially; medial parietal-interparietal suture recurved anteriorly between the separated temporal ridges (insertions of the posterior temporalis, 33/35 crania), which are raised in older individuals (fig. 9A, black arrow), or more rarely, the suture is nearly straight (2/35); squamosal expanded laterally into a broad shelf over the meatus (the insertion of the pars posterior of the temporalis muscle), such that the skull is much wider over the ear than at its narrower point posterior to the tip of the jugal (fig. 9A, white arrow). In dorsal view, the zygomatic arches generally narrow anteriorly. In lateral view, jugal robust and deep dorsoventrally; and squamosal forms a strong beaded ridge over the auditory meatus (fig. 7A). Upper incisors orange faced and extremely robust, with roots within the anterior maxillary base of the zygoma (posterior to a vertical line drawn from the anterior edge of the ascending arch). Many characters were reported in Iack-Ximenes et al. (2005), but others are first noted here.

NATURAL HISTORY: *Toromys grandis* appears to be restricted to seasonally or permanently flooded forests of *várzea* (white water) and *igapó* (black water) rivers. The BBC film "Amazon, Land of the Flooded Forest" shows two *T. grandis* using a treehole and traveling with monkey-like agility along branches in flooded forest (but it might have been filmed ex situ). Abreu-Júnior et al. (2017) twice saw *T. grandis* jump into the water and swim beneath the surface to escape when approached. *Toromys grandis* descends to terrestrial riverbanks, perhaps for mineral nutrients (fig. 14A), as does *Echimys saturnus* (see Blake et al., 2010). A recent image shows *T. grandis* feeding on green, unripe fruit of *Gustavia* sp. (Lecythidaceae) along the Rio Maués-Mirim about 70 km S of Urucurituba (fig. 1: loc. 16; J. Hall, personal commun.), and F. Reid (personal commun.) saw *T. grandis* feed on both leaves of a leguminous tree, and fruits. The large body size, robust cranium, and tendency in *Toromys* toward near-laminarity of the upper cheekteeth may be associated with a herbivorous or fibrous diet, as might the lateral expansion
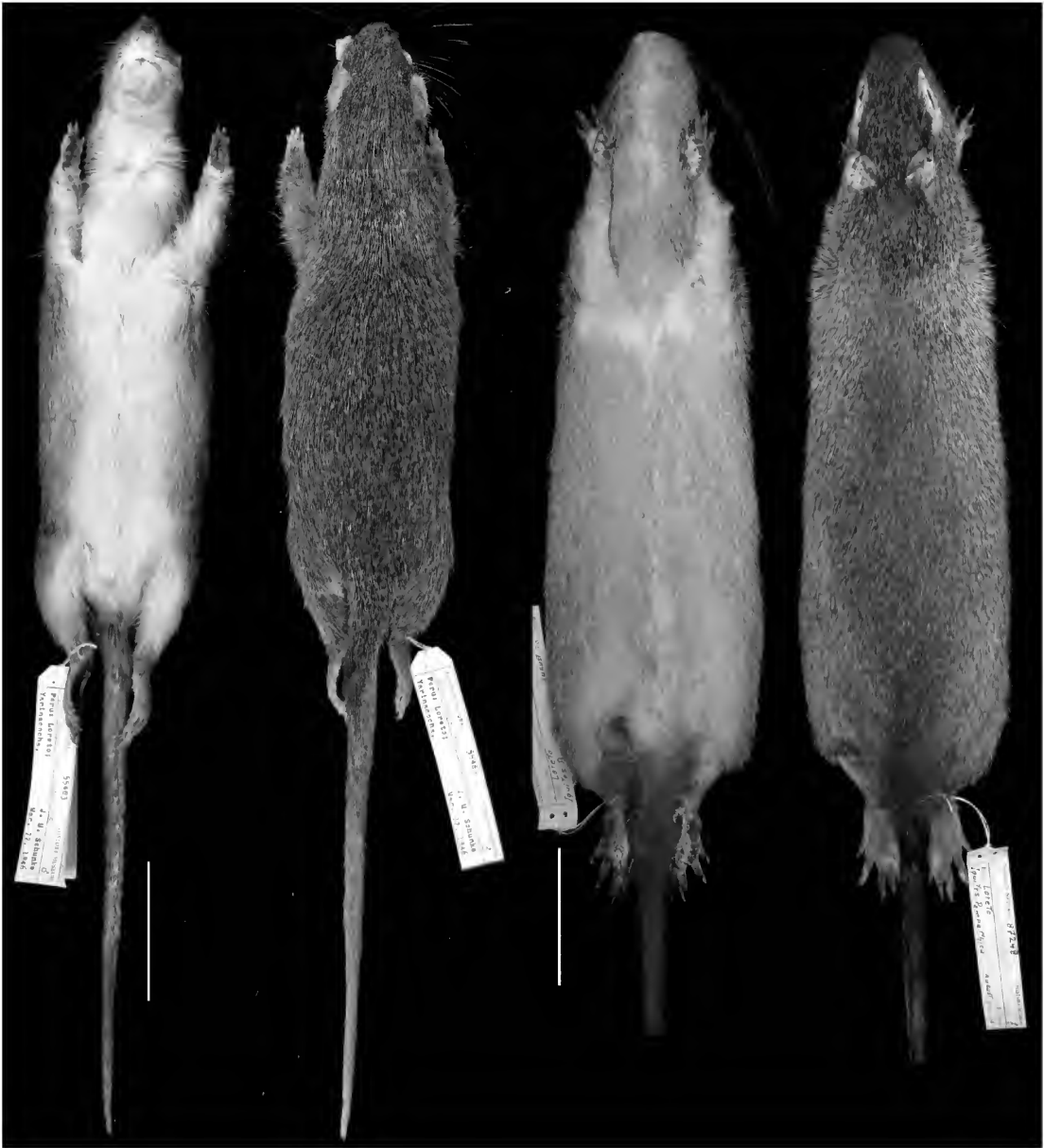
FIG. 16. *Toromys* skins, dorsal and ventral. *T. rhipidurus* FMNH 87248 (right), tail cropped during photography and rotated somewhat during preparation; *T. albiventris* FMNH 55483 (holotype; left), this skin is shrunken, the head and body lengths on the skin labels of the two taxa are approximately the same (table 5). Scale bar = 5 cm.

of the squamosal attachment of the temporalis muscle of *T. grandis* (fig. 9A), which is similarly expanded in the herbivorous "dactylomyines."

SPECIMENS EXAMINED: BRAZIL: *Amazonas*, Lago Manaquiri (NMW 920 [holotype]); Villa Bella Imperatriz (= Parantins), Santa Clara, Amazon River, south bank, (AMNH 92907, 92909–

92950, 93151–93153, 93594–93624, 93785, 93786); Serra do Parintins, Amazon River, south bank (not located); (AMNH 93625–93633, 94020–94036); Boca do Igarapé Piaba (MCZ 32352, 32353); Paraná de Faro, (BMNH 11.12.22.12); Santarém, (BMNH 5.6.3.1); Rio Amazonas, Ilha Urucurituba (FMNH 92198*, 92199); *Pará*, Faro, Fazenda Paraiso, (AMNH 37476); Faro, (AMNH 94037–94043); Villarinho do Monte, Rio Xingu, (AMNH 95957); Faro, Amazon River, north bank, Nhamundá River, Lago Uaimy, (AMNH 94193, 94194); Rio Nhamundá, Fazenda Paraiso, (FMNH 19497).

Toromys rhipidurus (Thomas, 1928)

Echimys rhipidurus Thomas, 1928: 291 (original description).

Type specimen and type locality: The holotype (by original designation, BMNH 28.7.21.89), an adult male skin and skull collected by R. W. Hendee on 25 January 1928 at "Pebas. Up. Amazons, 300′," Loreto, Peru.

Diagnosis and description: Much smaller than *Toromys grandis* (tables 5, 6), dorsum finely grizzled yellow-brown agouti heavily lined with black, sides paler yellowish; rostrum in front of and below the eyes, inner rear of thighs, dorsal and ventral tail base, and sometimes a lateral line are dull rust red-orange or red tinged (figs. 13B, 14C, 16). Small, pale yellow post-auricular patches are prominent in life, but not evident on most specimen skins (fig. 14C, 16). Aristiforms narrow, black or banded with ochraceous-buff subterminal bands, tipped dusky or ochraceous yellow (fig. 4E). Underparts pale gray-brown, sometimes with a white band between the elbows or white chest patches (fig. 16); gray color imparted by white-based and pale-tipped hairs with wide subterminal gray bands. Tail distal to the dorsal extension of body hair onto the base with long, monocolor black or dark rust-brown hairs above, which can nearly cover the scales proximally, but which shorten and thin distally to expose the scales at the tail tip, such that the tail appears conical; tail hairs paler laterally; self rusty at base below. Scales at dorsal tail base longer anterior-posteriorly than wide laterally, with strongly curved posterior edges (like fish scales, fig. 5C). Feet brown to grayish above; with sparse ungual tufts shorter than the strong claws. Plantar surfaces black pigmented, as for genus described above. Eyes mahogany brown, with pointed-ovoid, vertically slit pupils. Cranium robust, rostrum short and broad, and nasals slightly pinched in medially (fig. 9B). Jugal fossa deep and pointed anteriorly, with a strong ventral lip. Postglenoid fossa with or without a strong beaded lip of petrosal bone below. The space between the auditory meatus and ridge of squamosal above it as wide as or nearly the width of the meatus. Squamosal usually extends as a triangular tongue into the top of the mastoid process (fig. 7B). Medial parietal-interparietal suture between the temporal ridges generally strongly recurved anteriorly or with a medial notch (12/17), but can be straight (5/17, including the holotype). Upper molars with narrow lophs at right angles to the cranial axis, lophs notably parallel and of even width, and traversed by narrow parallel flexi in a distinctly laminar occlusal pattern (fig. 12D). First two lower molars with straight, angled posterolophids (fig. 12D). Incisor faces deep to medium orange; the upper incisor roots arise posterior to the anterior base of the maxillary zygoma.

NATURAL HISTORY. Little has been recorded of the habits of this species, other than that it is generally arboreal and can use tree hollows. A number of localities where specimens were collected are in white sand, "*varillal*" habitat (Río Nanay), a specialized ecosystem that harbors endemic plants and vertebrates (e.g., Alonso and Whitney, 2001).

SPECIMENS EXAMINED: PERU: *Loreto*, Pebas (BMNH 28.7.21.89 [holotype]); Río Napo, Lago Mirario (not located), (BMNH 32.8.4.21, 32.8.4.22); Boca Río Mazán, (BMNH 32.8.4.22a); Maynas, Puerto Indiana; (AMNH 73231, 73266–73277*, 73791); Orosa, Amazon River, (AMNH 74084–74086*); Genaro Herrera (= Jenaro Herrera), (AMNH 276710); Iquitos, Pampa Chica, (FMNH 87243, 87244*, 87245–87248); Río Nanay, Santa Rita, (FMNH 87249); Río Manití, Santa Cecilia (FMNH 87249–87252); Maynas, Quistococha, (FMNH 122991, 122992); Nazareth, Río Yavary, (FMNH 19854).

Toromys albiventris, sp. nov.

Echimys rhipidurus: Sanborn, 1949: 286 (a misidentification).
Makalata sp. nov. Emmons, 2005: 279.

HOLOTYPE: FMNH 55483, an adult male skin and skull, collected by José Schunke, 15 August 1946. The tail of the holotype is slightly bent at midpoint.

TYPE LOCALITY: Peru: Ucayali, Yarinacocha (8.35° S. 74.59° W; 155 m).

ETYMOLOGY: From the Latin *albus* ("white"), and *venter* ("belly"). The only *Toromys* with white underparts.

DIAGNOSIS: The smallest *Toromys*, with greatest length of skull 51.6–54.2 mm, and maxillary toothrow 10.1–11.9 mm (tables 5, 6). Dorsum coarse brown agouti, finely lined with black, tinted faintly rusty from behind shoulder to rump; aristiform hairs composed of narrow bristles with whiplike tips, mixed with some wider, spinelike aristifoms, also with hairlike tips (fig. 4F). Underparts sharply demarcated white, yellow-white, or beige-white, with faintly buffy areas (fig. 16). Tail shorter than head and body length; tail hair distal to the extension of the dorsal hair onto the base longer basally but does not cover scales, diminishes in length and pales in color down the length of the tail, tip thinly haired, with short, fine brown hairs. Incisors white or pale yellow. Nasal bones flare laterally posteriorly, to a variable extent. Mandible slender, with a shallow sigmoid notch, and coronoid process small and low.

DESCRIPTION: Dorsum coarsely grizzled brown-agouti, lined with black; back posterior to shoulders, flanks, ventral tail base, and hind limbs, are tinged rusty reddish; forequarters and head tinged more ochraceous yellow lined with black; extreme tip of muzzle dull rusty in some specimens, including the holotype (fig. 16), but barely so in others (fig. 13A). Dorsal hairs a mixture of several widths of wider and narrower bristlelike aristiforms, pale gray basally, banded black or dark brown, then buff or rusty, with dusky, buff, or rusty tips that are drawn out into long hairlike processes (fig. 4F). Hind feet rusty buff above, toes whitish; forefeet gray above. Claws unpigmented and small for the genus, silvery ungual tufts reach beyond their tips. Dorsal hair extends about 3.5 cm onto the tail base, colored like the back above, dull, unbanded rusty below. Posterior to the extension of body hair onto the tail base, tail hair is monocolor
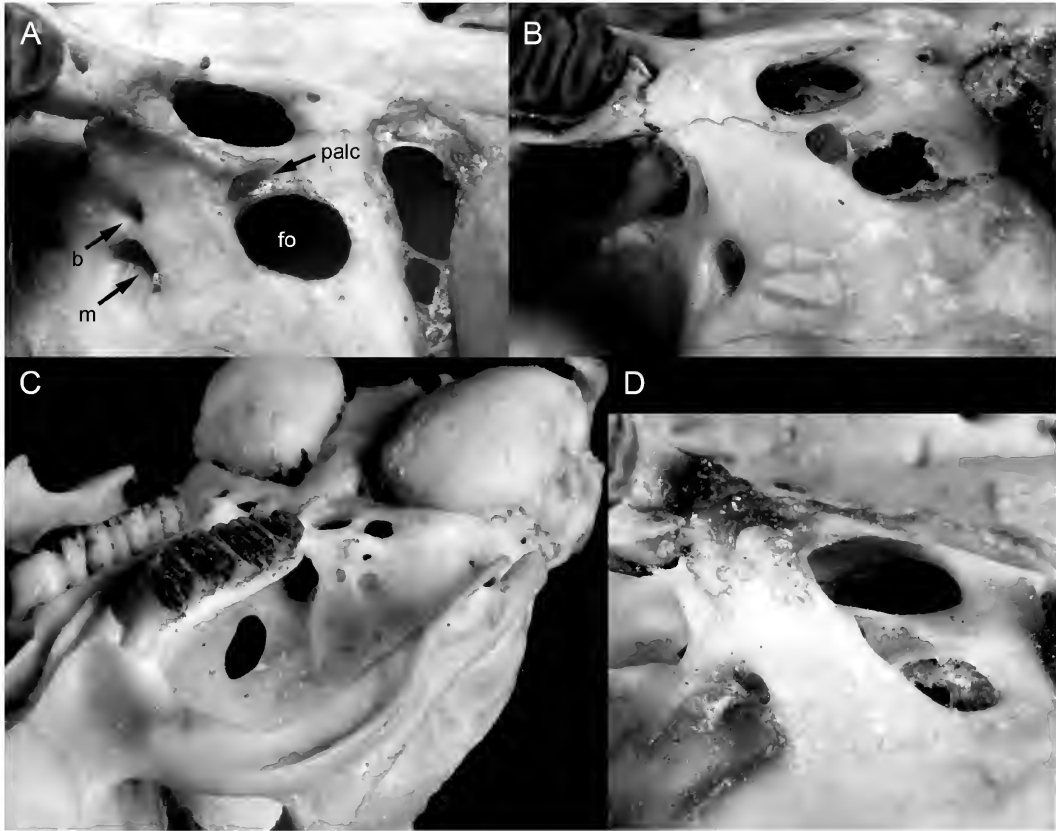
FIG. 17. *Toromys* species, right sides of basicrania. **A,** *T. albiventris* AMNH 98666; **B,** *T. grandis* AMNH 93604; **C,** *T. albiventris* holotype FMNH 55483; **D,** *T. rhipidurus* AMNH 73269. All specimens have separated masticatory and buccinator foramina. Note the separate, laterally opening palc in A and B; and in C the deep grooves and medial ridge extending onto the palate between the teeth. Abbreviations: **m,** masticatory foramen; **b,** buccinator foramen; **palc,** posterior opening of the alisphenoid canal; **fo,** foramen ovale.

black to brown dorsally, beige to white ventrally, over pigmented skin. Hairs longest at the dorsal base and midline, producing an indistinct keel to halfway down the tail, black or brown for about basal one-third, paling and diminishing gradually in length. Length of the tail hair varies between syntopic individuals, from distinctly to barely elongated. The longest hairs near the tail base reach across about five scale rows. Most tail hairs emerge from the scales in pairs, one longer and robust, the other shorter and finer. Tail scales squarish to hexagonal, about as long as wide, in uneven rows on dried skins. Underparts, including the sparsely haired inner limbs, white or slightly tinged yellowish or buff, with a grayish to gray-brown lateral band at the junction with the dorsal pelage. Throat and lower neck crossed by a faint buffy collar. One specimen, LSUMZ 8904, has ventral hairs with dusky subterminal bands lending a brownish tinge to the abdomen and with pale brownish bands across the lower throat and abdomen between the flanks, but the inner limbs are monocolored dirty white. Ear pinnae small, thinly haired inside with buffy hairs, with whitish or pale gray hairs behind; a few inconspicuous salient hairs extend from the rims. Mystacial vibrissae robust and black, the longest reach to

the shoulder when laid back; genal and supercilliary vibrissae fine and inconspicuous; ante-brachial vibrissae present. A female has two pairs of used lateral mammae, one above the flank and the other about midway between fore- and hind limbs and about 1.5 cm into the dorsal pelage field. The dried hindfeet appear unpigmented and relatively narrower across the base of the digits than are those of *T. rhipidurus*; they have small tubercles around and between the plantar pads, and collars around the digital pads, which appear large, but details of the feet are unclear. Forefeet with abundant small tubercles on the midline of the palm. Cranium in dorsal view with a long, slender braincase and a short rostrum; nasal bones pinched medially and flared laterally posteriorly and slightly anteriorly (fig. 9C). Parietal-interparietal suture nearly straight or bowed posteriorly; interparietal wide dorsally across the whole width of the posterior cranium. Incisive foramina slightly ovoid, widest anteriorly, with the maxillary and premaxillary portions of the septum broadly fused, and with a strong medial ridge leading onto the palate to between the premolar roots (figs. 7C, 17C). Supraorbital ridges beaded posteriorly, moderately expanded into shelves. Jugals dorsoventrally narrow, with jugal fossa narrow, and a slender insertion onto the maxillary. Incisors are white to pale yellow. Occlusal pattern as for the genus, but lophs and flexi of more uneven widths and angles, and M1 and M2 mures nearly at center of teeth. Unworn upper cheek teeth divided in half by the mesoflexus into two joined pairs of lophs (fig. 12A, B).

COMPARISONS WITH OTHER SPECIES: *Toromys albiventris* differs from *T. rhipidurus* by having more coarsely grizzled upperparts with more rust-tinged dorsum behind the shoulders (fig. 16), less rusty muzzles, shorter tail hairs, a white or pale-beige venter, slender foreclaws, and narrower hind feet. Compared to *T. rhipidurus* the cranium is more slender, with a narrower rostrum, narrower mesopterygoid notch, and the medial parietal-interparietal suture curved posteriorly rather than straight or recurved anteriorly.

LOCALITIES AND NATURAL HISTORY: The known specimens are from two localities (fig. 1). The type locality, Yarinacocha, is a left-bank oxbow lake of the Río Ucayali, a widely meandering, whitewater river, at about 150 m. Some of the Yarinacocha specimens were collected by J.M. Schunke in 1946, and the others were collected in the 1960s by expeditions from Louisiana State University. The second locality, "Suaya," is the origin of two specimens collected in 1926 by J.M. Schunke. Vaurie (1972) spelled this locality as "Suayo" and provided approximate coordinates of 07°18′ S; 74°55′ W, which is downstream and east of Contamana on the right bank of the Río Ucayali. We here emend this locality to Lagos del Suhaya, 7.46° S; 75.18° W; 160 m, left bank of the Río Ucayali, about 20 km WSW of Contamana. These are a group of lakes in a landscape depression that borders the meander zone of the river, and are likely accessible by boat during high water. This locality is on current maps, and is plausible because Schunke collected 10 days later at "Pampa Hermosa," a currently occupied and mapped village about 35 km downriver (north) of Contamana. Moreover, it is pronounced the same way as the original was written on the specimen label. None of the specimens are accompanied by habitat notes, but A.L. Gardner, collector of LSUMZ 14409 and LSUMZ 14408 (a *Makalata*), recalled in person to L.H.E. that both specimens were shot at night from the forest canopy, along the raised bank bordering a narrow channel leading into the west side of Yarinacocha lake, on the

northern outskirts of Pucallpa. The forest was disturbed, dense secondary regrowth, with large-diameter lianas. The two species were taken in the same stretch of trail. The region around Pucallpa is among the most heavily populated and deforested of the Peruvian Amazon, and now is crisscrossed by roads, plantations, and reservoir dams, and scarred from recent burns (Google Earth, 2017). Some gallery forests remain, likely because they are flood prone, and *T. albiventris* could be present in these. However, the right (east) bank of the Ucayali remains nearly entirely forested. Yarinacocha is a well-known ornithological locality from many LSUMZ expeditions (Stephens and Traylor, 1983).

REMARKS: Sanborn (1949) identified the 1946 FMNH specimens as *Toromys* ("*Echimys*") *rhipidurus*, but noted them as enigmatic, remarking correctly that the tail hair differed among specimens of the series. The two 1926 AMNH specimens are browner, with red-brown tail hairs paler than on those collected in 1946, and we suspect the older specimens have bleached to more orange hues. One collected in 1968 (LSUMZ 14409) has black dorsal tail hairs, while the 1962 specimen (LSUMZ 8904) has red-brown hairs that are scarcely elongated, but that form a slight dorsal keel along the tail. LSUMZ 8904, taken 31 July 1962, was multiparous and pregnant with a single, 30 mm embryo.

SPECIMENS EXAMINED: PERU: *Ucayali*, Yarinacocha (FMNH 55483, 55484, 55485, 55486, 55487, 62100, 62099, LSUMZ 8904, LSUMZ 14409*); Lagos del Suhaya (AMNH 98666*, 98667).

DISCUSSION

The variability of echimyid phenotypic characters makes it nearly essential to evaluate suspected new taxa in the family with molecular phylogenetics, which then allows the post hoc discovery of diagnostic morphological traits and the construction of plausible hypotheses about species units and phylogeny (e.g., see *Mesomys* and *Proechimys* in Patton et al., 2000). In this way, we have validated the previously suspected generic relationship of *T. albiventris* (see Emmons, 2005), confirmed those of *Toromys rhipidurus* and *Echimys saturnus*, and shown *Leiuromys occasius* to merit reclassifying (fig. 2). Although molecular relationships among genera of Echimyini are well supported (Loss and Leite, 2011; Upham et al., 2013; Upham and Patterson, 2015; Fabre et al., 2016b) and generally defined by morphological features such as cheektooth occlusal pattern (Patton et al., 2000; Leite 2003; Patterson and Velazco, 2008; Emmons, 2005), species identification by morphology has proven more intractable. Species within echimyine genera possess unique character combinations, but they have few unique elements, although species are often subjectively easily distinguishable (e.g., see character keys in Emmons and Feer, 1997; Emmons et al., 2015a), but sometimes not (Loss and Leite, 2011). We report some useful new characters of the feet and tail scales that seem consistent at the generic level, but again, these may not distinguish species (except perhaps in *Makalata*; fig. 6D, E). The soft tissues of fluid-preserved specimens clearly need more study: for example, the phallus has proved useful at the species level in *Phyllomys*, the largest genus (13–16 species, Leite, 2003: fig. 6; Emmons, 2005: fig. 10), but those of few taxa are documented, and soft tissues remain for the most part undescribed and present a field for future investigations.

With respect to genomics, there was little sequence divergence within our *Pattonomys* species samples, suggesting no unexpected or hidden population diversity (0.4%–0.7%; table 2), but a deeper intraspecific divergence among populations of *P. occasius* (2.0% of *cyt-b* uncorrected pairwise distance; table 2) and *Makalata* species samples (fig. 2), suggest unrecognized taxonomic diversity, the latter confirming the *cyt-b* results of Patton et al. (2000: 189).

Within the debate on the origins of the Neotropical biota, two recurrent hypotheses have been favored in recent years: (1) Andean biotas originated in the Amazon Basin (Bates and Zink, 1994; Hall, 2005; Brumfield and Edwards, 2007, Ribas et al., 2007); or (2) there was an Andean origin for Amazonian taxa (Patton et al., 2000; Haag et al., 2007; Santos et al., 2009). Echimyidae present useful biogeographical models for looking at Amazonian-Andean patterns of mammalian diversification (Upham et al., 2013; Fabre et al., 2016b). In their summary of Amazonian-Andean transitions of arboreal Echimyidae, Upham et al. (2013) showed that more lineages transitioned from Amazonia to the Andes than vice versa, especially during the Miocene (Upham et al., 2013: fig. 6). Our new mitogenomic samples contribute to the hypotheses of Upham et al. (2013). The most divergent *Toromys*, *Pattonomys*, and *Leiuromys* taxa are both small and found close to the Andean base (figs. 1, 2), whereas larger species appear to have more recently diverged and spread eastward along the Amazon (*T. grandis*) and Orinoco rivers (*P. carrikeri*, *P. punctatus*, *P. flavidus*). This is most notable among the three *Toromys*, where surprisingly, the headwater species *T. albiventris* is the most divergent molecularly (fig. 2, table 2). These phylogenetic patterns may reflect colonization of Brazilian Amazonia from the Andean base/Western Amazon Basin, perhaps associated with the formation of the Acre system (Hoorn et al., 2010). Dated molecular phylogenies have hypothesized that the basal split between Echimyini clades occurred in the late Miocene about 10–7 million years ago (Ma), when the Amazon River was being formed by Andean uplift (Hoorn et al., 2010; Upham et al., 2013, Upham and Patterson, 2015; Fabre et al., 2016b). Prior to 10 Ma the current Orinoco, Magdalena, and Amazonian systems were united in a vast "pan-Amazonian" region (Hoorn et al., 2010). These three systems comprise the currently isolated geographic ranges of the genera *Pattonomys* (Magdalena and Orinoco) and *Toromys* + *Leiuromys* (Amazonia), which likely diverged from a common ancestor as wetlands divided Pan-Amazonia: first, as the Pebas system (23–10 Ma), followed by the Acre system lake (10–7 Ma, Hoorn et al., 2010: fig. 1D). At the beginning of the Late Miocene, the entire current range of *T. rhipidurus* was under the waters of the Acre system while the uplifting Andean base (and Upper Ucayali) was dry. *Toromys* species might exemplify a western Amazonia/Andes origin, with a subsequent vicariance or dispersal to the eastern Amazonian riverine basin (*T. grandis*). A similar hypothesis was proposed for two other genera: *Dactylomys* and *Isothrix* (Patton et al., 2000, Upham and Patterson, 2015). However, our results show that *Echimys saturnus* from the Andean base is nested within a clade with both Amazonian (*Echimys*) and Atlantic Forest (*Phyllomys*) distributions. *Echimys saturnus* thus seems a recent western offshoot of this clade, which colonized or split from the eastern lineages of *Echimys* + *Makalata* + *Phyllomys*. However, more exten-

sive phylogeographic sampling is needed to test such a hypothesis. Indeed, both *Makalata* and *Echimys* have widespread distributions, and populations from both eastern and western Amazonia await taxonomic revision and phylogeographic analysis. Similarly, high sea levels or Andean uplift (see Fabre et al., 2016a, for further discussions) may have restricted the ancestral *Pattonomys* to the northern Andes, before declining sea levels after 2.5 Ma allowed easterly migration along the coast (Hoorn et al., 2010: fig. 1F). Compared to the divergence between *Toromys* species, *Pattonomys* species apparently diversified more recently into the northern Neotropical province (table 1).

The two groups of localities of *Leiuromys occasius* are about 1000 km apart, on either side of the ancient Acre system lake. It remains to be seen whether the gap is occupied by undiscovered populations, and whether there is morphological divergence between rats from the two regions. The presence of the Acre system lake to about 7 Ma might also account for the high genetic divergence between both *Makalata* and *Mesomys* species from east-central Bolivia, and populations in northern Peru (Patton et al., 2000; Orlando et al., 2003), and an apparent absence of *Makalata* species in the headwaters of the Río Madre de Dios.

Toromys and *Leiuromys* are taxa of evergreen humid forests, and within these, of riverine formations. The same is true of *Makalata*, *Dactylomys*, and *Isothrix* within Amazonia, but not of the last-named genus in the Guianas. The reason that floodplain forests are more favorable for some mammals is unclear, but is likely related to higher soil fertility, dry-season plant productivity, and sodium levels (Emmons, 1981; Hoorn et al., 2010; Peres, 2008). Soils derived from marine sediments of the Pebas and Acre formations produce mineral licks used by many herbivorous mammals, including *Echimys saturnus* (Blake et al., 2010; Bravo et al., 2012), and the vegetation there is likely higher in nutrients (Emmons and Stark, 1979). By contrast, *Pattonomys* species are among the most arid-adapted arboreal echimyids, along with *Phyllomys blainvillii*, *P. lamarum*, and *Makalata* sp. from the Caatinga biome. Marine aerosols provide coastal regions such as these and the Guiana Region littoral with higher mineral nutrients than are found in midcontinental soils (Bravo and Harms, 2016), while low rainfall reduces nutrient leaching. Environmental factors might thus constrain Echimyini to certain regions or subhabitats, superimposed on historical/biogeographical influences on their current distributions.

Apart from those of a few dactylomyines (Emmons, 1981; Silva et al., 2008), the behavior and ecological roles of arboreal Echimyidae are largely unknown. In situ, Echimyini other than *Dactylomys* are silent, tend to remain motionless when disturbed, and their dim eyeshine is difficult to see from below, so feeding is rarely documented (L.H.E., personal obs.). Recent use of thermal imaging to readily find echimyines and other nocturnal mammals in tropical forest canopies (J. Hall and F. Reid, personal commun.) shows promise for future natural history observations and specimen collection.

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REFERENCES

Abreu-Júnior, E.F.d., J.D. Charters, and A.R. Percequillo. 2017. The giant tree rat, *Toromys grandis* (Wagner, 1845): new record with range extension and comments on its morphology, biology and conservation. Mammalia. [doi.org/10.1515/mammalia-2017-0042]

Aguilera, M., N. Sanginés, and A. Pérez-Zapata. 1998. *Echimys semivillosus*, a rodent species with a very high chromosomal number. Caryologia 51: 181–187.

Allen, J.A. 1911. Mammals from Venezuela collected by Mr. M.A. Carriker, Jr., 1909–1911. Bulletin of the American Museum of Natural History 30 (10): 239–273.

Alonso, J.A., and B.M. Whitney. 2001. A new *Zimmerius* tyrannulet (Aves: Tyrannidae) from white sand forests of northern Amazonian Peru. Wilson Bulletin 113 (1): 1–9.

Bates, J.M., and R.M. Zink. 1994. Evolution into the Andes: molecular evidence for species relationships in the genus *Leptopogon*. Auk 111: 507–515.

Blake, J., D. Mosquera, J. Guerra, and D. Romo. 2010. New locality records and the first photographs of living *Echimys saturnus* (dark tree rat, Echimyidae) from eastern Ecuador. Ecotropica 16: 141–144.

Bravo, A., and K.E. Harms. 2016. The biogeography of sodium in neotropical figs (Moraceae). Biotropica 49 (1): 18–22.

Bravo, A., K.E. Harms, and L.H. Emmons. 2012. Keystone resource (*Ficus*) chemistry explains lick visitation by frugivorous bats. Journal of Mammalogy 93 (4): 1099–1109.

Brumfield, R.T., and S.V. Edwards. 2007. Evolution into and out of the Andes: a Bayesian analysis of historical diversification in *Thamnophilus* antshrikes. Evolution. 2007 (61): 346–367.

Capella-Gutiérrez, S., J.M. Silla-Martínez, and G. Toni. 2009. Trimal: A tool for automated alignment trimming in large-scale phylogenetic analyses. Bioinformatics 25: 1972–1973.

Carvalho, G.A.S., and L.O. Salles. 2004. Relationships among extant and fossil echimyids (Rodentia: Hystricognathi). Zoological Journal of the Linnean Society 142: 445–477.

Chapman, F.M. 1926. The distribution of bird-life in Ecuador: a contribution to a study of the origin of Andean bird-life. Bulletin of the American Museum of Natural History 55: 1–784.

Edgar, R.C. 2004. Muscle: multiple sequence alignment with high accuracy and high 1025 throughput. Nucleic Acids Research 32: 1792–1797.

Emmons, L.H. 1981. Morphological, ecological, and behavioral adaptations for arboreal browsing in *Dactylomys dactylinus* (Rodentia, Echimyidae). Journal of Mammalogy 62 (1): 183–189.

Emmons, L.H. 2005. A revision of the arboreal Echimyidae (Rodentia: Echimyidae, Echimyinae); with descriptions of two new genera. *In* E.A. Lacey, and P. Myers (editors), Mammalian diversification: from chromosomes to phylogeography: 247–309. Berkeley: University of California Press.

Emmons, L.H., and F. Feer. 1997. Neotropical rainforest mammals: a field guide, 2nd ed. Chicago: University of Chicago Press.

Emmons, L.H., and N. Stark. 1979. Elemental composition of a natural mineral lick in Amazonia. Biotropica 11: 311–313.

Emmons, L.H., Y.L.R. Leite, D. Kock, and L.P. Costa. 2002. A review of the named forms of *Phyllomys* (Rodentia: Echimyidae) with the description of a new species from coastal Brazil. American Museum Novitates 3380: 1–40.

Emmons, L.H., Y.L.R. Leite, and J.L. Patton. 2015a. Family Echimyidae Gray, 1825. *In* J.L. Patton, U.F.J. Pardiñas, and G. D'Elía (editors), Mammals of South America, vol. 2. Rodents: 877–950. Chicago: University of Chicago Press.

Emmons, L.H., Leite, Y.L., and Patton, J.L. 2015b. Genus *Toromys* Iack-Ximenes, de Vivo, and Perciquillo. *In* J.L. Patton and U.F.J. Pardiñas (editors), Mammals of South America, vol. 2. Rodents: 929–31. Chicago: University of Chicago Press.

Fabre, P.-H., L. Hautier, D. Dimitrov, and E.J. Douzery. 2012. A glimpse on the pattern of rodent diversification: a phylogenetic approach. BMC Evolutionary Biology 12 (88): 1–19.

Fabre, P.H., T. Galewski, M.-K. Tilak, and E.J. Douzery. 2013. Diversification of South American spiny rats (Echimyidae): a multigene phylogenetic approach. Zoologica Scripta 42 (2): 117–134.

Fabre, P.-H. et al. [7 authors]. 2014. Rodents of the Caribbean: origin and diversification of hutias unravelled by next-generation museomics. Biology Letters 10 (7): 20140266.

Fabre, P.-H., J.L. Patton, Y.L.R. Leite. 2016a. Family Echimyidae (Hutias, Coypu and South American spiny-rats). *In* D.E. Wilson, T.E. Lacher, and R.A. Mittermeier (editors), Handbook of Mammals of the World, vol. 6. Rodents and Lagomorphs: 552–564. Barcelona: Lynx Editions.

Fabre, P.-H. et al. [10 authors]. 2016b Mitogenomic phylogeny, diversification, and biogeography of South American spiny rats. Molecular Biology and Evolution. 34 (3): 613–633.

Galewski, T., J.-F. Mauffrey, Y.L.R. Leite, J.L. Patton, and E.J.P. Douzery. 2005. Ecomorphological diversification among South American spiny rats (Rodentia; Echimyidae): a phylogenetic and chronological approach. Molecular Phylogenetics and Evolution 34: 601–615.

Geoffroy Saint-Hilaire, I. 1838. Notice sur les rongeurs épineux désignés par les auteurs sous les noms d'*Echimys, Loncheres, Heteromys* et *Nelomys*. Comptes Rendus Hebdomadaires de l'Académie des Sciences 6 (26): 884–888.

Geoffroy Saint-Hilaire, I. 1840. Notice sur les rongeurs épineux, designés par les auteurs sous les noms d'*Echimys, Loncheres, Heteromys* et *Nelomys*. Magasin de Zoologie, d'Anatomie Comparée et de Palaeontologie 1840 (Series 2): 1–57 +10 pl.

Gouy, M., S. Guindon, and O. Gascuel. 2010. Seaview version 4: a multiplatform graphical user interface for sequence alignment and phylogenetic tree building. Molecular Biology and Evolution 27 (2): 221–224.

Guilderson, T., L. Burckle, S. Hemming, and W. Peltier. 2000. Late Pleistocene sea level variations derived from the Argentine shelf. Geochemistry, Geophysics, Geosystems 1: Paper number 2000GC000098.

Haag, T., et al. [6 authors]. 2007. Phylogenetic relationships among species of the genus *Calomys* with emphasis on South American lowland taxa. Journal of Mammalogy 88 (3): 769–776.

Hall, J.P.W. 2005. Montane speciation patterns in *Ithomiola* butterflies (Lepidoptera: Riodinidae): are they consistently moving up in the world? Proceedings of the Royal Society of London, Series B, Biological Science 272: 2457–2466.

Handley, C.O., Jr. 1976. Mammals of the Smithsonian Venezuelan Project. Brigham Young University Science Bulletin 20: 1–89 + map.

Hollister, N. 1914. Descriptions of four new mammals from tropical America. Proceedings of the Biological Society of Washington 27: 141–144.

Hoorn, C. et al. [10 authors]. 2010. Amazonia through time: Andean uplift, climate change, landscape evolution, and biodiversity. Science 330: 927–931.

Iack-Ximenes, G.E., M. De Vivo, and A.R. Percequillo. 2005. A new genus for *Loncheres grandis* Wagner, 1845, with taxonomic comments on other arboreal echimyids (Rodentia, Echimyidae). Arquivos do Museu Nacional, Rio de Janeiro 63 (1): 89–112.

Kearse M. et al. [11 authors]. 2012. Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. Bioinformatics 28: 1647–1649.

Lara, M.C., J.L. Patton, and M.N.F. da Silva. 1996. The simultaneous diversification of South American echimyid rodents (Hystricognathi) based on complete cytochrome *b* sequences. Molecular Phylogenetics and Evolution 5: 403–413.

Lartillot, N., and H. Philippe. 2004. A Bayesian mixture model for across-site heterogeneities in the amino-acid replacement process. Molecular Biology and Evolution, 21 (6): 1095–1109.

Lartillot, N., T. Lepage, and S. Blanquart. 2009. PhyloBayes 3: a Bayesian software package for phylogenetic reconstruction and molecular dating. Bioinformatics 25: 2286–2288.

Leite, Y.L.R. 2003. Evolution and systematics of the Atlantic tree rats, genus *Phyllomys* (Rodentia, Echimyidae), with description of two new species. University of California Publications in Zoology 132: 1–118 + xv.

Leite, Y.L.R., and J.L. Patton. 2002. Evolution of South American spiny rats (Rodentia, Echimyidae): the star-phylogeny hypothesis revisited. Molecular Phylogenetics and Evolution 25: 455–464.

Loss, A.C., and Y.L.R. Leite. 2011. Evolutionary diversification of *Phyllomys* (Rodentia: Echimyidae) in the Brazilian Atlantic Forest. Journal of Mammalogy 92: 1352–1336.

Loss, A.C., R.T. Moura, and Y.L.R. Leite. 2014. Unexpected phylogenetic relationships of the painted tree rat *Callistomys pictus* (rodentia: Echimyidae). Natureza on Line 12: 132–136.

Meyer, M., and M. Kircher. 2010. Illumina sequencing library preparation for highly multiplexed target capture and sequencing. Cold Spring Harbor Protocols 2010: 5448.

Monteiro, L.R., V. Bonato, and S.F. Dos Reis. 2005. Evolutionary integration and morphological diversification in complex morphological structures: mandible shape divergence in spiny rats (Rodentia, Echimyidae). Evolution and Development 7: 429–439.

Orlando, L., et al. [6 authors]. 2003. Napoleon Bonaparte and the fate of an Amazonian rat: new data on the taxonomy of *Mesomys hispidus* (Rodentia: Echimyidae). Molecular Phylogenetics and Evolution 27: 113–120.

Patterson, B.D., and P.M. Velazco. 2006. A distinctive new cloud-forest rodent (Hystrignognathi: Echimyidae) from the Manu Biosphere Reserve, Peru. Mastozoologia Neotropical 13 (2): 175–191.

Patterson, B.D., and P.M. Velazco. 2008. Phylogeny of the rodent genus *Isothrix* (Hystricognathi, Echimyidae) and its diversification in Amazonia and the eastern Andes. Journal of Mammalian Evolution 15: 181–201.

Patton, J.L., and M.A. Rogers. 1983. Systematic implications of non-geographic variation in the spiny rat genus *Proechimys* (Echimyidae). Zeitschrift für Säugetierkunde 48: 363–370.

Patton, J.L., M.N.F. da Silva, and J.R. Malcolm. 2000. Mammals of the Rio Juruá and the evolutionary and ecological diversification of Amazonia. Bulletin of the American Museum of Natural History 244: 1–306.

Paynter, R.A., Jr. 1993. Ornithological gazetteer of Ecuador, 2nd ed. Cambridge, MA: Museum of Comparative Zoology (Harvard University).

Paynter, R.A., Jr., and M.A.J. Traylor. 1991. Ornithological gazetteer of Brazil, Cambridge, MA: Museum of Comparative Zoology, (Harvard University).

Pelzeln, A. von. 1883. Brasilische Säugetiere. Resultate von Johann Natterer's Reise in den Jahren 1817 bis 1835. Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien 33 (Suppl.): 1–140.

Peres, C.A. 2008. Soil fertility and arboreal mammal biomass in tropical forests. *In* W. Carson and S. Schnitzer (editors), Tropical forest community ecology: 349–364. Malden, MA: Wiley-Blackwell.

Pictet, F.-J. 1843. Seconde notice sur les animaux nouveaux ou peu connus du musée de Genève. Mémoires de la Société de Physique et d'Histoire Naturelle de Genève 10 (1): 201–213.

Ranwez, V., S. Harispe, F. Delsuc, and E.J.P. Douzery. 2011. Macse: Multiple alignment of coding sequences accounting for frameshifts and stop codons. PLoS ONE 6: e22594.

Ribas C.C., R.G. Moyle, C.Y. Miyaki, J. Cracraft. 2007. The assembly of montane biotas: linking Andean tectonics and climatic oscillations to independent regimes of diversification in *Pionus* parrots. Proceeding Royal Society B Biological Science 274: 2399–2408.

Sanborn, C.C. 1949. Mammals from the Rio Ucayali, Peru. Journal of Mammalogy 30: 277–288.

Santos, J.C., et al. [6 authors]. 2009. Amazonian amphibian diversity is primarily derived from late Miocene Andean lineages. PLoS Biology 7 (3): e1000056.

Silva, R.B., M.V. Emerson, and P. Izar. 2008. Social monogamy and biparental care of the Neotropical southern bamboo rat (*Kannabateomys amblyonyx*). Journal of Mammalogy 89 (6): 1464–1472.

Smithe, F.B. 1975. Naturalist's color guide. New York: American Museum of Natural History.

Stamatakis, A. 2006. RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. Bioinformatics 22 (21): 2688–2690.

Stephens, L., and M.A.J. Traylor. 1983. Ornithological gazetteer of Peru. Cambridge, MA: Museum of Comparative Zoology (Harvard University).

Tate, G.H.H. 1935. The taxonomy of the genera of Neotropical hystricoid rodents. Bulletin of the American Museum of Natural History 68 (5): 295–447.

Thomas, O. 1899. On new small mammals from South America. Annals and Magazine of Natural History (7) 3: 152–155.

Thomas, O. 1921. New *Sigmodon*, *Oryzomys*, and *Echimys* from Ecuador. Annals and Magazine of Natural History (9) 7: 448–450.

Thomas, O. 1928. The Godman-Thomas expedition to Peru.–viii. On mammals obtained by Mr. Hendee at Pebas and Iquitos, upper Amazons. Annals and Magazine of Natural History (10) 2: 285–294.

Tilak, M.-K., et al. [6 authors]. 2015. A cost-effective straightforward protocol for shotgun illumina libraries designed to assemble complete mitogenomes from non-model species. Conservation Genetics Resources 7: 37–40.

Upham, N.S., and B.D. Patterson. 2015. Evolution of caviomorph rodents: a complete phylogeny and timetree for living genera. *In* A.I. Vassallo, and D. Antenucci (editors), The biology of Caviomorph rodents: diversity and evolution: 63–120. Buenos Aires: SAREM.

Upham, N.S., R. Ojala-Barbour, J. Brito, P.M. Velazco, and B.D. Patterson. 2013. Transitions between Andean and Amazonian centers of endemism in the radiation of some arboreal rodents. BMC Evolutionary Biology 13: 191, 24 pp.

Vaurie, C. 1972. An ornithological gazetteer of Peru (based on information compiled by J.T. Zimmer). American Museum Novitates 2491: 1–36.

Voloch, C.M., J.F. Vilela, L. Loss-Oliveira, and C.G. Schrago. 2013. Phylogeny and chronology of the major lineages of New World hystricognath rodents: insights on the biogeography of the Eocene/Oligocene arrival of mammals in South America. BMC Research Notes 6 (160): 1–9.

Voss, R.S. 1992. A revision of the South American species of *Sigmodon* (Mammalia, Muridae) with notes on their natural history and biogeography. American Museum Novitates 3050: 1–56.

Wagner, J.A. 1845. Diagnosen einiger neuen Arten von Nägern und Handflügern. Archiv für Naturgeschichte 11: 145–149.

Wahlert, J.H. 1974. The cranial foramina of protrogomorphous rodents: An anatomical and phylogenetic study. Bulletin of the Museum of Comparative Zoology 146: 363–410.

Wiley, R.H. 2010. Alfonso Olalla and his family: the ornithological exploration of Amazonian Peru. Bulletin of the American Museum of Natural History 343: 1–68.

Woods, C.A., and E.B. Howland. 1979. Adaptive radiation of capromyid rodents: Anatomy of the masticatory apparatus. Journal of Mammalogy 60: 95–116.

APPENDIX 1

GAZETTEER OF MAPPED LOCALITIES (FIG. 1)

Localities in the lists that follow are grouped by species, country, and next-largest administrative unit (state or department), in that order, and coordinates are provided in decimal degrees. If unavailable from specimen labels or field notes, geographic coordinates were sourced chiefly from ornithological gazetteers (Stephens and Traylor, 1983; Paynter and Traylor, 1991; Paynter, 1993) or other publications (Handley, 1976; Voss, 1992; Abreu-Júnior et al., 2017), where further information may be available. For a few, apparently unpublished, localities, Google Earth (2017) was used to acquire coordinates and elevations of named localities (e.g., Río Jatunyaco, 800 m and 750 m).

Toromys albiventris
PERU
1. Ucayali: Yarinacocha (-8.3, -74.6).
2. Ucayali: Suaya (= Lagos de Suhaya) (-7.458, -75.185).

Toromys rhipidurus
PERU
3. Loreto: Iquitos, Pampa Chica (-3.8, -73.2).
4. Loreto: Río Nanay, Santa Rita (-3.8, -73.5).
5. Loreto: Río Manití, Santa Cecilia (-3.4, -72.8).
6. Loreto: Quistococha (-3.8, -73.3).
7. Amazonas: Nazareth, Río Yavary (opposite Remate de Males, Brazil) (-4.34, -70.32).
8. Loreto: Orosa (-3.433, -72.133).
9. Loreto: Pebas (-3.33, -71.82).
10. Loreto: Boca Mazán (-3.4520, -72.7279).
11. Loreto: Puerto Indiana (-3.4667, -73.05).
12. Loreto: Jenaro Herrera (-4.9056, -73.6686).

Leiuromys occasius
ECUADOR
31b. Pichincha: Gualea (considered erroneous) (-0.1167, -78.8333).
33. Napo: Río Jatunyacu 750 m (-1.0817, -77.8691).
34. Napo: Río Jatunyacu 800 m (-1.0833, -77.9667).
37. Napo: Río Suno Abajo (-0.7046, -77.2407).
PERU
35. Loreto: Mouth of Río Santiago (-4.4667, -77.6156).
36. Loreto: Boca Río Curaray (-2.3662, -74.9359).
32. Madre de Dios: Río Colorado, zona boca (-12.65, -70.3333).
38. Madre de Dios: Cocha Cashu (seen by LHE) (-11.88, -71.41).

Toromys grandis
    BRAZIL
        14. Amazonas: Lago do Batista, Rio Amazonas (-3.2833, -58.2667).
        15. Amazonas: Lago Manaqueri, Rio Solimões (-3.4833,-60.5167).
        16. Amazonas: Urucurituba, Rio Amazonas (-2.7667,-57.8167).
        17. Pará: Santarém, Belterra (-2.6333, -54.9333).
        18. Pará: Bravo, N bank Rio Amazonas (-1.9, -55.167).
        19. Pará: Faz Recreio, Ilha Caviana (-0.1667, -50.1667).
        20. Pará: Gran Lago Cuiteua, north bank Rio Amazonas (-1.8167, -54.9667).
        21. Pará: Gran Parana do Bom Jardim (-2.0333, -56.2).
        22. Pará: Parana de Faro (-2.1667, -56.7333).
        23. Pará: Santarém (-2.4333, -54.7).
        24. Pará: Obidos (-1.9167, -55.5167).
        25. Pará: Santa Rita, Rio Amazonas (-2.0333, -55.3).
        26. Amazonas: Villa Bella Imperatrix (= Parantins) (-2.6, -56.44).
        27. Pará: Boca do Igarapé Piaba (-1.55, -55.32).
        28. Pará: Faro (-2.11, -56.44).
        29. Pará: Fazenda Paraiso, Rio Nhamundá (-2.11, -56.44).
        30. Pará: Villarhino do Monte (-1.37, -52.01).
        31. Amazonas: Rio Purus (fig. 14A, photo) (-5.828, -63.156).

Pattonomys carrikeri
    VENEZUELA
        40. Guárico, Zaraza (9.35, -65.3167).
        41. Guárico: Río Orituco, 10 km W of Chaguaramas (9.4, -66.4667).
        42. Lara: Caserio Boro, 10 km N of El Tocuyo, 520m (9.47, -69.48).
        43. Lara: San Miguel, Hacienda La Fortuna (9.53, -69.31).
        44. Lara: Río Tocuyo, (10.16, -69.48).
        45. Carabobo: Montalbán, 1.2 km SE Montalbán, El Castaño (10.2, -68.33).
        46. Carabobo: San Esteban (10.4333, -68.0167).
        47. Carabobo: Puerto Cabello (10.47, -68.43).
        48. Distrito Federal: Caracas (10.5, -66.9167).
        49. Falcón: 19 km NW Urama, km 40 (10.617, -68.4).
        50. Falcón: Coro (11.4167, -69.6833).
        51. Apure: Puerto Paez, 38 km NNW, Río Cinaruco (6.55, -67.5167).
        52. Bolívar: Caicara, Río Orinoco (7.6464, -66.1722).
        53. Bolívar: Hato La Florida, 44 km SE of Caicara (7.5, -65.78).

Pattonomys semivillosus
    COLOMBIA
        54. Magdalena: Atlántico, opposite Barranquilla, lower Río Magdalena (10.9833, -74.8).

55. Bolívar: Cartagena (10.4167, -75.533).
56. Bolívar: Morales, Río Viejo (8.5833, -73.85).
57. César: Valledupar, El Orinoco Río César (10.4833, -73.25).
58. César: Río Guaimaral, Valledupar, Río Garupal (9.8167, -73.6167).

Pattonomys flavidus
   VENEZUELA
   59. Nueva Esparta: Margarita Island, El Valle (10.9833, -63.8667).